

Dr. F. E. Davis Indianapolis. Dept. of Botany

Butler University Botanical Studies

Volume XI

Papers 8-17

November, 1954

MEMORIAL ISSUE

Dedicated to the memory of

DR. RAY C. FRIESNER

by the former majors in the Botany Department of Butler University (1920-1952) and by his colleagues on the faculty of Butler University.

UNIVERSITY OF HAWAII
LIBRARY

TABLE OF CONTENTS

Volume XI, Papers 8-17

Dr. Ray C. Friesner

Dr. Friesner, Botanist-Teacher
J. JOHANNA JONES (pp. 103-104)

Dean Ray C. Friesner, a Tribute from the Faculty of Liberal Arts
(pp. 104-106)

Bibliography of the late Ray C. Friesner
(pp. 107-111)

CONTRIBUTED MEMORIAL PAPERS

Temperature Inversions in the Pinyon-Juniper Zone of a
Nevada Mountain Range.
W. D. BILLINGS (pp. 112-118)

Alpine Timberlines in the Americas and their Interpretation.
R. DAUBENMIRE (pp. 119-136)

Hepaticae from the Federal District, Mexico. I.
DOROTHY PARKER (pp. 137-138)

Preservation of some Algal Cultures by Lyophilization.
W. A. DAILY and J. M. McGuIRE (pp. 139-143)

A Rare *Tolypella* New to the United States of America.
FAY KENOYER DAILY (pp. 144-148)

Quantitative Relationships of Terrestrial Mosses with some
Coniferous Forests at Mt. Rainier National Park.
N. HIGINBOTHAM and BETTY WILSON HIGINBOTHAM
(pp. 149-168)

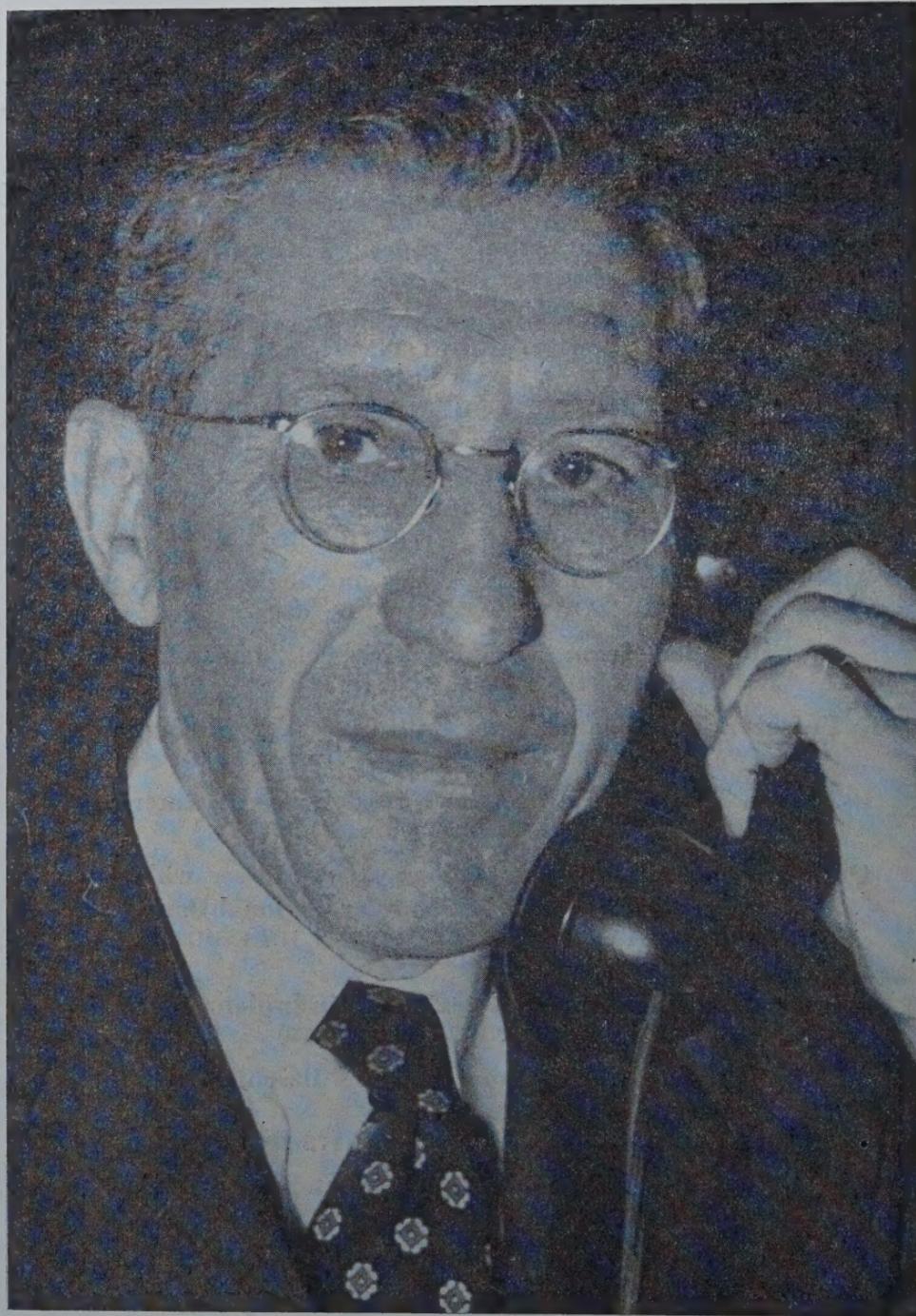
An Interesting Megaspore Species Found in Indiana Block Coal.
G. K. GUENNEL (pp. 169-177)

Re-evaluation of the Diatom Species *Nitzschia frustulum*
(Kutz.) Grun.
CHARLES W. REIMER (pp. 178-191)

Expression of the Gene *d₁* in the Scutellum of Maize.
JEANETTE S. PELTON (pp. 192-198)

Post-Algonquin and Post-Nipissing Forest History of
Isle Royale, Michigan.
J. E. POTZGER (pp. 199-208)

(All Authors, except J. M. McGuire and Jeanette S. Pelton, were Students of
Dr. Ray C. Friesner.)



DR. RAY C. FRIESNER

FEBRUARY 8, 1894 - DECEMBER 1, 1952

DR. FRIESNER, BOTANIST-TEACHER

By J. JOHANNA JONES, Butler 1952

With the passing of Dr. Ray C. Friesner, Indiana has lost one of her most active field botanists and teachers. For more than thirty years, Dr. Friesner hiked the woods and fields of Indiana, collecting and identifying plants to swell the records of Indiana flora. As a teacher and scientist, he inspired many students with his example of industry, study, and vision.

Dr. Friesner was born in 1894 at Bremen, Ohio. He worked his way through high school, and received his A.B. from Ohio Wesleyan University in 1916, and his Ph.D. from the University of Michigan in 1919. During the summers of 1918 and 1919 he was instructor at the University of Michigan. In the fall of 1919 he became assistant professor of botany in the Biology Department of Butler University, Indianapolis. The following year he became head of the new Department of Botany; in 1947 he was appointed Dean of the College of Liberal Arts and Sciences, and retained both positions until his death on December 1, 1952.

Shortly after his arrival in Indiana he met Dr. Charles C. Deam, nationally-known Indiana botanist and author of "Flora of Indiana" and other books on Hoosier plants. Dr. Friesner became vitally interested in field taxonomy as practiced by Dr. Deam, and with his characteristic energy and thoroughness set about collecting and identifying every species of higher plant hitherto unreported for Indiana or for the county in which it was found. His collections total 25,500 and swelled the Butler University herbarium. Not only a general taxonomist, Dr. Friesner was a widely recognized authority on the goldenrods, on which he published monographs. In connection with his field work, he compiled each year the Indiana Plant Distributions Records, supplements to Deam's "Flora of Indiana."

A leader in the Indiana Academy of Science, Dr. Friesner was secretary from 1926 to 1935, and president in 1936. He was active on many of the Academy committees and in the botany, taxonomy, and history of science meetings. One of his most recent contribu-

tions was an index of the Indiana Academy of Science Proceedings from 1941 to 1950.

During his more than thirty years of service to the Botany Department at Butler University, Dr. Friesner supervised the development of the departmental library and the *Butler University Botanical Studies*. The latter is a publication presenting original research performed mainly in Indiana. In normal times it is distributed to libraries scattered throughout the world. Under his direction the department has expanded from a total of three courses offered at the time of its origin, to a total of twenty-seven listed in the current catalog.

In addition to his numerous duties as administrator, teacher, and scientist, Dr. Friesner was active in the Indianapolis Downey Avenue Christian Church, and was chairman of the official Board of Directors there. He was teacher of a Philathea class for more than twenty years. He held membership in the American Association for the Advancement of Science, the American Association of University Professors, the American Genetic Association, the Botanical Society of America, Phi Beta Kappa, Phi Sigma, Phi Kappa Phi, the Eugenics Research Association, and the Academies of Science of the states of Illinois, Indiana, and Ohio. In 1948 Dr. Friesner was the recipient of the James Irving Holcomb Award at Butler University. In 1951 he received the D.Sci. degree from Ohio Wesleyan University. He has been cited in Indiana Men of Science, American Men of Science, and Who's Who in America.

Dr. Friesner will long be remembered among his associates for his traits of honesty, industry, kindness, and devotion to duty. His record is not contained only in the lists of his publications, offices, and honors, but must be measured also by the ranks of students whom he inspired with his teaching and by his example and companionship. He has erected his own memorial within the hearts of those who knew him.

DEAN RAY C. FRIESNER

The moral and intellectual greatness of a University depends primarily upon the qualities of heart and mind which animate the men who make and direct its policies and teach its students. That man is touched by sublimity whose life is marked at once by love of God,

Man, and of Nature, and who renders to each a just tribute. Such a one was Ray C. Friesner, of late our Dean and Colleague in this Faculty.

Dean Friesner exemplified the Christian gentleman and intelligent man of good will in public and private life. His teaching, research and publication, administrative skill, and his service to students, University, and science were distinguished by broad perspective and careful regard for minutiae. He was learned in Scripture and by the Word of God he regulated his own life and guided wisely the young men and women whose good fortune it was to work with him.

Dr. Friesner saw the wonders of the natural world around him as manifestations of the greatness and goodness of God, and like Agassiz and Shaler, he learned its secrets and made them known to others. For thirty-three years he directed the growth of the Department of Botany at Butler University. He established an herbarium expanded now to nearly 100,000 sheets. He was second to none in his native state as a field botanist and taxonomist. Through the editorship of the *Butler University Botanical Studies*, he made known the fruits of Indiana research to scholars and libraries all over the world. He had been called to the presidency of the Indiana Academy of Science and he had directed the Division of Graduate Studies of this University. In 1951 his work was crowned with the degree of doctor of science awarded *in honoris causa* by his alma mater.

The fine quality of Dr. Friesner's intellect was revealed by his characteristic insight, patience, self-denial, persistence, and humility. Its versatility was demonstrated in council and classroom, in field and forest, in laboratory and library. The measure of his academic renown is found in the able colleagues who surrounded him, in the talented students he taught to take his place, in his long list of publications, in the unsought honors bestowed upon him by institutions and scholarly societies, and in the high esteem of his friends.

The Dean of the College of Liberal Arts and Sciences was a man of great goodness of heart who possessed a singular capacity to awaken in others a desire to emulate the good. And perhaps only his bereaved wife and venerable father can attest fully to the loving affection he brought to his home. The world of science and Butler

University, together with all his colleagues in this Faculty, mourn his passing. A sincere and loyal friend, a distinguished scientist and teacher, a gifted and humane administrator, a man greatly loved, has passed beyond the portals of this campus.

THE FACULTY

THE COLLEGE OF LIBERAL ARTS AND SCIENCES

A. Dale Beeler,
Secretary

Indianapolis, Ind.
9 January 1953

BIBLIOGRAPHY OF THE LATE RAY C. FRIESNER

HEAD, DEPARTMENT OF BOTANY (1920-1952)

BUTLER UNIVERSITY

1. FRIESNER, R. C. Daily rhythm of elongation and cell division in certain roots. *Am. Jour. Bot.* 7:380-407. 1920.
2. FRIESNER, R. C. AND STANLEY A. CAIN. Some ecological factors in succession: upland hardwoods I. Evaporation studies in the Sycamore Creek region. *Butler Univ. Bot. Stud.* 1:1-15. 1930.
3. FRIESNER, RAY C. The genus *Trillium* in Indiana. *Butler Univ. Bot. Stud.* 1:29-40. 1930.
4. _____ AND STANLEY A. CAIN. Some ecological factors in secondary succession: upland hardwoods II. Soil reaction and plant distribution in the Sycamore Creek region. *Butler Univ. Bot. Stud.* 1:17-28. 1930.
5. _____. Key to the ferns and fern allies. *Butler Univ. Bot. Stud.* 1:55-60. 1931.
6. _____. Chromosome numbers in ten species of *Quercus* with some remarks on the contribution of cytology to taxonomy. *Butler Univ. Bot. Stud.* 1:77-104. 1930.
7. CAIN, STANLEY A., RAY C. FRIESNER AND J. E. POTZGER. A comparison of strip and quadrat analyses of the woody plants on a central Indiana river bluff. *Butler Univ. Bot. Studies.* 1; 157-171. 1931.
8. CAIN, STANLEY A. AND RAY C. FRIESNER. Certain aspects of the H-ion concentration of the soils of a central Indiana bluff. *Butler Univ. Bot. Stud.* 1:172-175. 1931.
9. FRIESNER, RAY C. A microtome cooler. *Butler Univ. Bot. Stud.* 1:176. 1932.
10. FRIESNER, RAY C. AND J. E. POTZGER. Studies in forest ecology. I. Factors concerned in hemlock reproduction in Indiana. *Butler Univ. Bot. Stud.* 2:133-143. 1932.

11. ———. Studies in forest ecology. II. The ecological significance of *Tsuga canadensis* in Indiana. *Butler Univ. Bot. Stud.* 2:144-150. 1932.
12. FRIESNER, RAY C. The genus *Solidago* in northeastern North America. *Butler Univ. Bot. Stud.* 3:1-64. 1933.
13. FRIESNER, RAY C. AND J. E. POTZGER. Climax conditions and the ecological status of *Pinus strobus*, *Taxus canadensis*, and *Tsuga canadensis* in the Pine Hills region of Indiana. *Butler Univ. Bot. Stud.* 3:65-84. 1934.
14. POTZGER, J. E. AND RAY C. FRIESNER. Some comparisons between virgin forest and adjacent areas of secondary succession. *Butler Univ. Bot. Stud.* 3:85-98. 1934.
15. KLEINE, ARNOLD, J. E. POTZGER AND RAY C. FRIESNER. The effect of precipitation and temperature on annual ring growth in four species of *Quercus*. *Butler Univ. Bot. Stud.* 3:199-206. 1936.
16. FRIESNER, RAY C. AND J. E. POTZGER. Soil moisture and the nature of the *Tsuga* and *Tsuga-Pinus* forest association in Indiana. *Butler Univ. Bot. Stud.* 3:207-209. 1936.
17. ——— ———. Contrasts in certain physical features in *Fagus-Acer* and *Quercus-Carya* communities in Brown and Bartholomew counties, Indiana. *Butler Univ. Bot. Stud.* 4:1-12. 1937.
18. FRIESNER, RAY C. Indiana as a critical botanical area (Presidential address). *Proc. Indiana Acad. Sci.* 46:28-45. 1937.
19. POTZGER, J. E. AND RAY C. FRIESNER. Plant migration in the southern limits of Wisconsin glaciation in Indiana. *Amer. Midl. Nat.* 22:351-368. 1939. (Part of symposium before the Taxonomy Section, AAAS).
20. FRIESNER, RAY C. Key to species and varieties of ferns and fern allies of northeastern North America. *Butler Univ. Bot. Stud.* 4:141-162. 1940.
21. POTZGER, J. E. AND RAY C. FRIESNER. A phytosociological study of the herbaceous plants in two types of forests in central Indiana. *Butler Univ. Bot. Stud.* 4:163-180. 1940.

22. _____ What is climax in central Indiana? A five-mile quadrat study. *Butler Univ. Bot. Stud.* 4:181-195. 1940.

23. FRIESNER, RAY C. Some necessary nomenclatorial changes in the genus *Solidago*. *Butler Univ. Bot. Stud.* 4:196. 1940.

24. _____. A study of asymmetrical growth from stump sections of *Quercus velutina*. *Butler Univ. Bot. Stud.* 4:197-206. 1940.

25. _____. A preliminary study of growth in beech, *Fagus grandifolia*, by the dendrograph method. *Butler Univ. Bot. Stud.* 5:85-94. 1941.

26. _____ AND GLADYS M. FRIESNER. Relation of annual ring formation to rainfall as illustrated in six species of trees in Marshall County, Indiana. *Butler Univ. Bot. Stud.* 5:95-112. 1941.

27. _____. The genus *Solidago* in West Virginia. *Castanea* 6:59-75. 1941.

28. _____. Nomenclatorial changes in the genus *Solidago*. *Butler Univ. Bot. Stud.* 5:113-116. 1942.

29. _____. Vertical growth in four species of pines in Indiana. *Butler Univ. Bot. Stud.* 5:145-159. 1942.

30. _____. Dendrometer studies on five species of broadleaf trees in Indiana. *Butler Univ. Bot. Stud.* 5:160-172. 1942.

31. POTZGER, J. E., RAY C. FRIESNER AND CARL KELLER. Phytosociology of the Cox woods: a remnant of forest primeval in Orange County, Indiana. *Butler Univ. Bot. Stud.* 5:190-221. 1942.

32. FRIESNER, RAY C. Some aspects of tree growth. *Proc. Indiana Acad. Sci.* 52:36-44. 1943.

33. FRIESNER, RAY C. Correlation of elongation in primary, secondary and tertiary axes of *Pinus strobus* and *P. resinosa*. *Butler Univ. Bot. Stud.* 6:1-9. 1943.

34. POTZGER, J. E. AND RAY C. FRIESNER. An ecological survey of Berkey woods: a remnant of forest primeval in Kosciusko County, Indiana. *Butler Univ. Bot. Stud.* 6:10-16. 1943.

35. FRIESNER, RAY C. Two *Solidago* hybrids worthy of names. *Butler Univ. Bot. Stud.* 6:81-83. 1943.
36. FRIESNER, RAY C. AND CHARLES M. EK. Correlation of micro-climatic factors with species distribution in Shenk's woods, Howard County, Indiana. *Butler Univ. Bot. Stud.* 6:87-101. 1944.
37. ————— AND J. E. POTZGER. Survival of hemlock seedlings in a relict colony under forest conditions. *Butler Univ. Bot. Stud.* 6:102-115. 1944.
38. —————. The Cabin Creek raised bog, Randolph County, Indiana. *Butler Univ. Bot. Stud.* 8:24-43. 1947.
39. FRIESNER, RAY C. AND GEORGE H. SMITH. Fifty-year index of Proceedings of Indiana Acad. Sci. pp. 1-289. 1948.
40. ————— AND GERSHOM WALDEN. A five-year dendrometer record in two trees of *Pinus strobus*. *Butler Univ. Bot. Stud.* 8:1-23. 1947.
41. POTZGER, J. E. AND RAY C. FRIESNER. Forests of the past along the coast of southern Maine. *Butler Univ. Bot. Stud.* 8:178-203. 1948.
42. FRIESNER, RAY C. Two new entities in the genus *Solidago*. *Butler Univ. Bot. Stud.* 9:124-126. 1949.
43. —————. Growth-rainfall and trend-co-efficients shown by six species of hardwoods in Brown County, Indiana. *Butler Univ. Bot. Stud.* 9:159-166. 1950.
44. ————— AND JOHANNA JONES. Correlation of elongation in primary and secondary branches of *Pinus resinosa*. *Butler Univ. Bot. Stud.* 10:119-152. 1952.
45. —————. The pioneer period in the study of Indiana's vascular flora. *Butler Univ. Bot. Stud.* 10:144-152. 1952.
46. —————. Cumulative index Proceedings Indiana Academy of Science, vols. 51-60. *Proc. Indiana Acad. Sci.* 61:359-453. 1951.
47. —————. (posthumous) Rafinesque and the taxonomy of Indiana vascular plants. *Butler Univ. Bot. Stud.* 11:1-4. 1953.

NOTE: Dr. Ray C. Friesner had been in charge of Indiana plant distribution records I to XIII (1939-1952). They have appeared in the Proceedings of the Indiana Academy of Science for these years.

His laboratory manual for general botany, in mimeographed form, was used at Butler for 32 years.

Deam's Flora of Indiana carries the name of Ray C. Friesner eleven times in the bibliography. Under the genus *Solidago* Dr. Deam says: "The following key has been adapted from Friesner's study, *The genus Solidago in Northeastern North America*. Grateful acknowledgment is given."

On September 6, 1944, Dr. Ray Friesner was honored by the former botany majors at a special 25th anniversary celebration, commemorating the quarter century of botany at Butler University. Volume VII of *Butler Univ. Bot. Stud.* pays tribute to that event.

THANK YOU!

For the Botany alumni we express sincere thanks to Florence Geisler and Evelyn Hoober for service on the contact committee, as well as to the Phi Kappa Phi City Chapter and to the faculty of Liberal Arts College for financial contributions to this memorial number of the *Butler University Botanical Studies*.

TEMPERATURE INVERSIONS IN THE PINYON-JUNIPER ZONE OF A NEVADA MOUNTAIN RANGE

By W. D. BILLINGS

Department of Botany, Duke University, Durham, North Carolina

Prominent on the sides of the Great Basin mountain ranges of Nevada is an open woodland zone of small conifers in which the dominants are pinyon (*Pinus monophylla* T. and F.) and juniper (*Juniperus osteosperma* (Torr.) Little). It is apparent even to the casual observer that this dark green zone is almost entirely restricted to the slopes; the grayish sagebrush-valley bottoms are treeless except for willows and cottonwoods along the drainages. Also treeless are most of the ridges and peaks which rise above the two or three thousand vertical feet covered by the woodland. Within the dwarf conifer zone, even small valleys, bowls, and flats are open and sagebrush-covered. Around the edges of most of the valleys and depressions, the bronze-green junipers form a prominent border with relatively few pinyons, but higher on the slopes the gray-green pinyon dominates, often in pure stands.

In 1948, preliminary investigations were begun on the ecology of the pinyon-juniper zone. In the autumn of that year, maximum-minimum thermometers and rain gauges were set up across a small valley near the crest of the Virginia Mountains southeast of Reno. One station was located on the pinyon-covered south-facing slope at an elevation of about 6675 feet, another at the same elevation on the north-facing slope about 400 yards across the valley and in similar vegetation, while the third station was in the relatively flat bottom of the valley and about 200 feet lower in elevation. The latter area was sagebrush-covered with only a few scattered junipers and an occasional pinyon. The air thermometers were installed at a height of 2 feet on the north sides of tree trunks. The thermometers and rain gauges were read at intervals of 3 or 4 weeks for a year and then the instruments were moved to new locations.

Since there are practically no climatic data from weather stations in the pinyon-juniper zone of Nevada, it was decided to install ther-

mometers and rain gauges just inside the lower and upper elevational limits of the zone on the west side of the Virginia Range and also in the region of maximum development of the vegetation near the middle of the zone. This was done in October, 1949, and the stations continued in operation until May, 1953. A total of six stations was set up on north- and south-facing slopes of ridges at elevations of 4825 feet, 5640 feet, and 6780 feet. The air thermometers were placed in open aluminum shelters on the north sides of tree trunks at heights of 1 meter above the ground. Readings were made at intervals of 3 or 4 weeks for most of the 3 years and 8 months of the study's duration. Only an analysis of the air temperature data from these two studies is reported here.¹

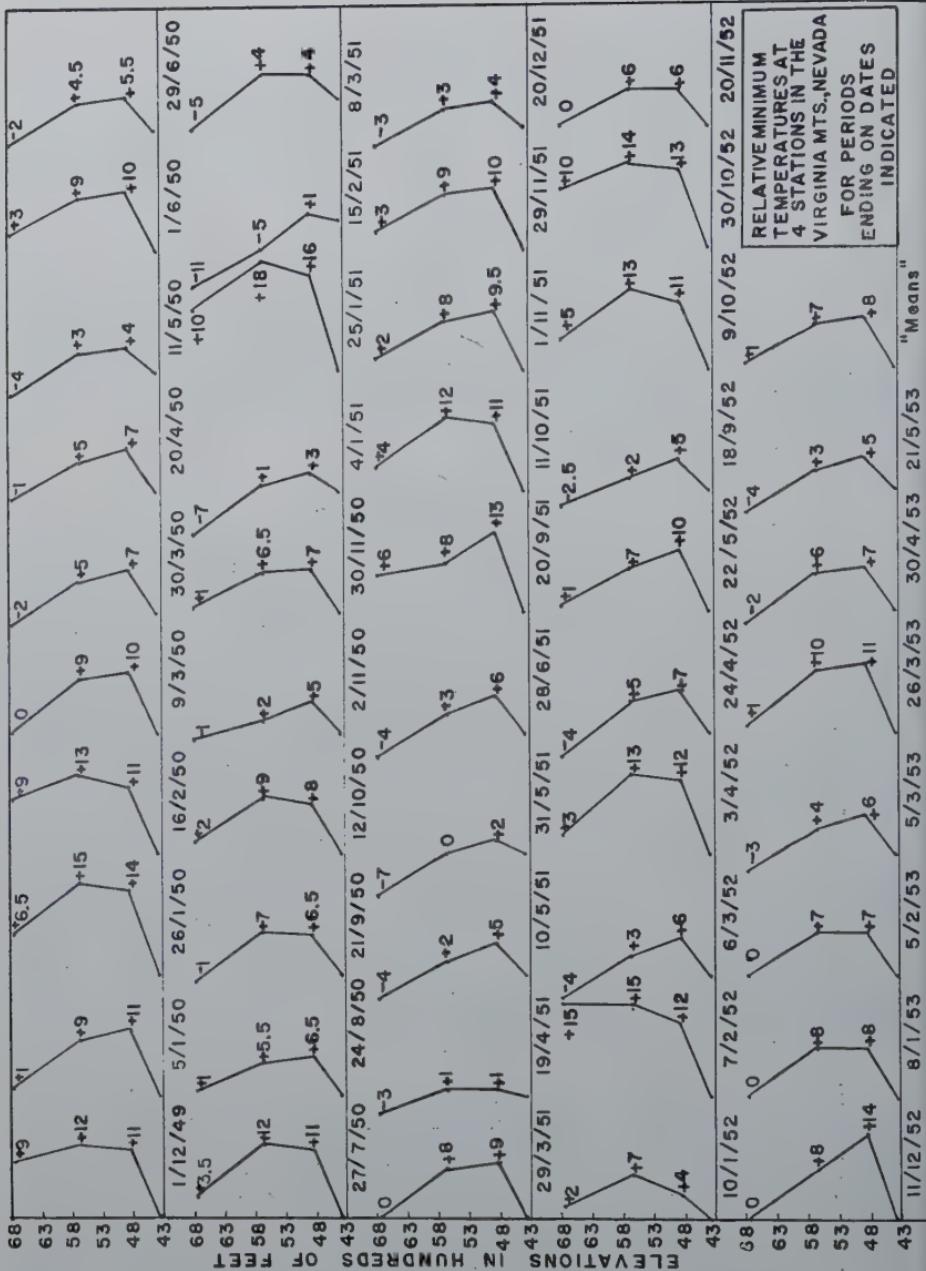
RESULTS

An analysis of the air temperature data in comparison with those from the official U. S. Weather Bureau station at Hubbard Field in the sagebrush valley bottom shows immediately that the most prominent feature of the temperature climate is an inversion of minimum temperatures on the sides of the mountain range. This produces a thermal belt which is practically coincidental with the pinyon-juniper zone and, of course, is the result of cold air drainage into the valley at night through the sparsely vegetated canyons. It seems to be present most of the time throughout the year in the early morning hours as indicated in Figure 1 since a single cold night at the normal lapse rate in the 3 or 4 weeks of a measurement period would eradicate the records of the inversion on the maximum-minimum thermometers. This apparently occurred only once or twice during the entire period of observation.

Using the minimum temperature in the valley bottom (at 4397 feet) as zero, the relative minimum temperatures of the south-facing stations are plotted for each period in Figure 1. Temperatures at north-facing stations at the same elevations are not plotted here; they are usually a degree or two colder than those at the south-facing stations except occasionally in the summer. However, the inversion is so marked (often as much as 10° to 18° F.) at the 4825 foot and

¹ It is a pleasure to acknowledge the assistance of the many ecology students at the University of Nevada whose cheerful cooperation made the servicing of the stations possible.

Fig. 1



5640 foot stations that the north-facing slopes at these elevations are also almost always warmer at night than the level valley bottom. Only near the upper edge of the zone, 2400 feet above the valley, do the minimum temperatures approach those of the valley bottom.

The layer of cold air in the valley bottom is apparently not very deep since the mean minimum only 425 feet above was 8° higher. Very early on a cold winter morning, the cold air part of the inversion is indicated by the depth of the smoke haze over Reno; it appears to be less than 200 feet deep and often under 100 feet.

Maximum temperatures in the valley bottom and at the 4825 and 5640 foot levels are almost identical. This results in a smaller diurnal temperature range in the pinyon-juniper than in the sagebrush of the valley floor. However, maximum temperatures at the 6780 foot level are distinctly cooler, usually being 10° to 15° lower than those at Hubbard Field.

Temperatures recorded in 1948 and 1949 across the small valley high in the range are shown in Table I together with those from the Reno station (Hubbard Field) in the bottom of the valley to the west of the range. While both slopes are usually warmer than Reno even though almost 2300 feet higher, the small flat between them was always colder than Reno. This was an unusually severe winter for the region and during the coldest weather, minimum temperatures in the small flat were usually 12° to 13° colder than the below-zero temperatures only 200 feet above on the slopes.

DISCUSSION

In mountainous western North America, particularly in the drier parts with sparse vegetation, temperature inversions are probably not rare (see Shreve 1914 for southern Arizona, Young 1920, 1921 for southern California and southern Oregon, and Hayes 1941 for northern Idaho). Baker (1944) points out that in many parts of the West such inversions tend to mask any relation between lowest observed temperatures and elevation. However, Price and Evans (1937) in central Utah found little temperature inversion in a series of weather stations ranging from 5575 to 10100 feet on the west front of the Wasatch Plateau. Nevertheless, there is a dearth of information on such inversions and resultant thermal belts since most Weather Bureau stations are located in the fertile and flat valley bottoms. This is particularly true of the Great Basin across its 500 mile width. In fact, Baker states that climatic data are so scanty for this region that no altitudinal temperature trends can be determined.

TABLE I
Minimum and maximum temperatures (°F.) across a small flat-bottomed valley near crest of Virginia Mountains, Nevada, with comparative data from Reno.

Sta.	Elev.	14.10-48	4.11-48	2.12-48	6.1-49	17.2-49	17.3-49	7.4-49	28.4-49	19.5-49	Means* for period
		to 4.11-48	to 2.12-48	6.1-49	to 17.2-49	17.3-49	7.4-49	to 28.4-49	19.5-49	to 13.10-49	
Minimums											
S-facing	6675 ft.	20	15	-1	-6	21	15	31	27	24	16.2
Flat	6475 ft.	13	5	-14	-18	9	9	21	22	18	7.2
N-facing	6675 ft.	21	14	-4	-8	18	16	33	27	22	15.4
Reno	4397 ft.	14	7	-7	-16	20	16	25	28	22	12.1
Maximums											
S-facing	76	67	52	50	60	64	74	75	75	94	68.0
Flat	71	61	51	51	66	75	73	73	91	91	67.2
N-facing	67	56	50	46	56	62	74	71	93	93	63.9
Reno	79	70	56	60	66	72	81	82	98	98	73.8

* Both mean minimum and mean maximum temperatures are somewhat weighted downward because of the greater frequency of winter readings over summer readings.

It may be significant that the mean altitudinal limits of the thermal belt on the west side of the Virginia Range correspond very closely to the upper and lower limits of the pinyon-juniper vegetation on this range. Certainly other factors are involved in restricting pinyon-juniper to the slopes, such as the possible detrimental effects of alluvium on growth of the conifers, precipitation totals, and especially depth and persistence of snow at the upper levels. Further data are needed on the possible relationships between the lower edge of the pinyon-juniper and the variation in depth of the cold valley air at critically low temperatures. During the very cold winter of 1948-1949, pinyon showed considerable cold damage and some winter-killing around the edges of some of the western Nevada valleys particularly to the south of the study area. Low soil moisture was also a factor at this time because of two years of drought.

In this region, the average depth of the thermal belt appears to be about 2000 to 2200 feet. More information is needed on the elevation having highest minimum temperatures. Apparently, on the ridges, this is close to 1000 feet above the valley floor. It would not be surprising if such thermal belts exist on most of the mountain ranges of the central and western Great Basin since the Virginia Range topography and vegetation are rather typical of the mountain ranges of most of Nevada south of the Truckee and Humboldt Rivers.

SUMMARY

Maximum and minimum temperatures were measured for 3 years and 8 months at 6 stations located near the lower edge, in the middle, and near the upper edge of the pinyon-juniper zone in the Virginia Mountains of western Nevada. Temperatures were measured for an additional year across a small valley near the crest of the range. Comparison with temperatures for the same periods in the sagebrush-covered valley to the west of the range shows that minimum temperatures in the valley bottom are as much as 10° to 15° colder than those on the slopes 400 to 1300 feet above. These inversions seem to be present for most of the year and also occur in small valleys within the range itself. The resultant thermal belt above the layer of cold night air seems to be coincidental with the pinyon-juniper zone in this mountain range.

LITERATURE CITED

BAKER, F. S. 1944. Mountain climates of the western United States. *Ecological Monog.* 14: 223-254.

HAYES, G. L. 1941. Influence of altitude and aspect on daily variations in factors of forest-fire danger. *U. S. Dept. Agr. Circ.* 591, 38 pp.

PRICE, R., AND R. B. EVANS. 1937. Climate on the west front of the Wasatch Plateau in central Utah. *Monthly Weather Rev.* 65: 291-301.

SHREVE, F. 1914. The role of winter temperatures in determining the distribution of plants. *Amer. Jour. Bot.* 1: 194-202.

YOUNG, F. D. Effect of topography on temperature distribution in southern California. *Monthly Weather Rev.* 48: 462-463.

_____. 1921. Nocturnal temperature inversions in Oregon and California. *Monthly Weather Rev.* 49: 138-148.

ALPINE TIMBERLINES IN THE AMERICAS AND THEIR INTERPRETATION

By R. DAUBENMIRE

The State College of Washington

The literature of plant geography has long contained references to the facts that (1) in progressing from the poles toward the equator, alpine timberline increases in elevation above sea level, and that (2) the elevation of this timberline exhibits considerable variation at any one latitude on different mountain systems (Gannett, 1899; Smiley, 1921). More recently a third fact concerning the geography of this vegetation boundary has been documented; the latitude-altitude relationship is not rectilinear (Herzog, 1931; Daubenmire, 1943; Troll, 1948).

In the present paper the writer has undertaken to summarize all the published information on the elevation of American alpine timberlines that is available to him, the dry timberlines at the bases of the Cordilleras being completely ignored, in order to bring these three phenomena into sharper focus. Because of the extreme scarcity of prerequisite climatologic data, and the unavailability of most of these to the writer, no extended inquiry into the etiology of alpine timberline can be attempted. However, after describing the geographic facts, the principle theories as to the causes of upper timberline on mountains will be briefly reviewed in relation to certain data compiled with reference to alpine timberlines of North America.

ALTITUDINAL CHARACTERISTICS OF AMERICAN TIMBERLINES

In assembling data on the elevation of alpine timberlines at specific locations, one often finds considerable variation in values given by different authors for the same area. This may be attributed to (1) differences among writers as to whether they have given the elevation of the *forest line* (the upper edge of continuous forest), the *tree line* (the altitude of the highest stunted tree), or a point midway across this zone of transition between forest and alpine tundra, which is the interpretation favored by the writer. Additional discrepancies

undoubtedly have arisen out of the fact that the elevation of timberline is influenced to a certain extent by the direction of exposure, by the height and proximity of surrounding mountains, and by soil. Because of all these complications, latitude-altitude curves of timberline elevations as compiled from the literature require much smoothing, but even so, well-defined trends are revealed.

In Figure 1 are four curves based upon records assembled from scattered publications and from the writer's field notes. The short line A represents the altitudinal relations of timberline from Maine to New York. Only within this region are the Appalachians high enough to have a climatically determined upper timberline comparable with that of the Cordilleras.* Records for the high mountains along the Pacific coast from Prince William Sound, Alaska, to the southern Sierra Nevada Mountains of California, are indicated by + signs and represented by smoothed line B. Curve C represents the mean altitude of alpine timberline along the divide of the Cordillera from the arctic tundra to the equator. Curve D is redrawn from Troll (1948) who presented a diagram considered typical of the earth, combining data from Eurasia and Mexico to represent the northern hemisphere.

Figure 2 contains a continuation of line C in Figure 1 from the equator southward to Tierra del Fuego, based on the few separate accounts available to the writer. Line D is a continuation of Troll's diagram which is based on data from all parts of the southern hemisphere. Line E represents forest limits in the easterly range of the Andes, and F the same for the westerly ranges, both being redrawn from Herzog (1931). The gap in those curves based entirely on South American data is occasioned by the treeless segment (puna) of the Andes which finds no counterpart in North America.

* Timberlines of the southern tip of the Appalachians have the characteristics of climatic timberlines, but the altitude is far too low to fit into the otherwise harmonious altitudinal pattern of North American timberlines, and the climatic limitation appears to be of a very special character. These bald summits are probably no more than analogous with the usual type of montane timberline. In the writer's opinion, the closest homolog of these balds are the grass-covered southwest exposures of steep bluffs in forested regions just east of the mid-continental grassland. For highly suggestive meteorologic studies of the southern Appalachians, see Donley & Mitchell (1939).

In spite of discrepancies in the data from different sources, several facts seem well established. First, along the main axis of the Cordilleras, the altitude of upper timberline increases from the arctic and antarctic regions toward the equator to about the 30° parallel in the northern hemisphere, or the 25° parallel in the southern hemisphere, at which points the curves tend to flatten abruptly. From these points of flexure toward the equator, the altitude of timberline is rather constant except for a slight dip centered on the equator.

Secondly, upper timberlines on the three most important mountain axes in North America show the same north-south cant in temperate latitudes of approximately 110m per degree of latitude. There is a strong suggestion that the cant of timberline in temperate South America is essentially the same.

A third major conclusion is that where they may be compared along the same parallel, the elevation of alpine timberline in North America is lowest in the Appalachians, highest along the continental divide, and intermediate on the mountains near the Pacific coast.

Finally, timberlines in temperate South America are lower on ranges adjacent to the coast in comparison with others farther inland, which is likewise true in the extratropical Cordillera of North America and on low mountains in northeastern Canada (Hustich, 1954), but the reverse of the situation in tropical South America. As Herzog (1931) points out, the rule which fits all these cases is that alpine timberlines are lower on the wetter side of a major mountain system.

THE ETIOLOGIC PROBLEM

To the long-standing problem of the etiology of upper timberlines from the autecologic viewpoint, there may now be added three relatively new ones of geographic scope. We now need an explanation of the break in the altitude-latitude curves which falls at 30° and 25° in the north and south hemispheres, respectively. Also, the differences in elevation of timberlines on different mountain systems that cross the same meridian present a challenge, as does the reversal of this relationship within the Cordillera of South America.

The solution of these problems must be founded upon two bodies of facts, both of which are far from complete. One of these is

autecologic and concerns the evaluation of factor complexes that become inimical to trees above certain altitudes. The other is information on the altitudinal and latitudinal variations in climatic conditions.

Each of the tree taxa which forms a part of timberline in different parts of the world unquestionably has its own special limits of tolerance of the climatic vicissitudes of high mountains. The fact that timberline curves for the Americas exhibit such general uniformity of elevation over wide area, even though wholly distinct floras are involved, points to the existence of an important but as yet unknown ecologic principle. The relationship might well prove analogous to that of plants and the wilting coefficient of the soil, in which the environmental force withholding water abruptly increases beyond the absorbing capacities of all plants even though these capacities are variable. Another fact which may be interpreted as indicative of the existence of a principle of broad significance is that the many genera which form alpine timberline are represented by evergreen taxa at this ecotone.* Therefore, the evergreen habit appears more closely adapted to the peculiar climatic limitation than is the deciduous. If this view is correct, that potential differences in timberline elevation attributable to genetic differences among the trees involved are submerged beneath some fundamental environmental force that is most nearly compensated by evergreeness, the universality of the phenomenon would appear to immeasurably reduce the complexity of the ultimate explanation. This concept is in accord with the conclusion

* If the subalpine *Betula tortuosa* forests of the Scandinavian mountains appear to provide an exception to this generalization, the view may be taken that here in northwest Europe the circumpolar *Picea-Abies-Betula* forest has been decimated by glaciation so recently that nothing more fundamental is involved than the temporary (in the geologic sense) loss of local ecotypes of the two evergreen genera which nearly everywhere else in the northern hemisphere are conspicuous at alpine timberline. Referring back to the bald summits of the southern Appalachians, the historical factor cannot be used here, for the area immediately to the north and at comparable elevation, contains *Picea rubens*, *Abies fraseri*, and *Betula lutea*. The transition from temperate forest to grassland without intervening taiga, coupled with a conspicuous lack of widespread alpine floristic elements, may be taken as evidence that this grassland should not be placed in the same phytogeographic category as tundra. In certain parts of southern Europe, deciduous angiosperm forests also extend to upper timberline, as in the southern Appalachians, but taiga is the more usual type of forest here (Schröter, 1926).

of Hustich (1952) who considers the ecology of trees at the subarctic timberline to be "almost the same" even though different taxa form different segments of the line. It should be noted, however, that this opinion stands in sharp contrast to that of J. Braun-Blanquet (1951, p. 135) who considers alpine timberline not to be climatically equivalent throughout for the reason that the different taxa involved have different ecologic amplitudes.

TIMBERLINE THEORIES*

Excessive light. Collaer (1934, 1940) has championed the theory that in the Alps the upward increase in light intensity impairs leaf functions and in this way is critical in setting the upward altitudinal limits of taxa and consequently of forests.

The writer knows of no source of climatic data in the Americas which would permit a critical test of the applicability of this theory to the problems under consideration, but there is a special situation that has an important bearing upon them. Maps published in "Climate and man" (U.S.D.A., 1941) show that the peninsula of oceanic climate which extends far inland into western North America along the Canada-U.S.A. border crosses both the Cascades and the Rockies. The number of hours of sunshine both in winter and summer (pp. 738, 739) is reduced, the average number of cloudy days (p. 743) is increased, and the number of days with dense fog (p. 737) is increased in this peninsula. If any component of solar radiation were rather directly related to the cause of timberlines, the curves in Figure 1 should be deflected in this latitude, but such does not appear to be the case. It must also be noted that Collaer resorts to dry winds or low winter temperatures to explain the fact that timberline elevations in the Alps vary within short space in such a fashion that the light hypothesis alone is inadequate.

Carbondioxide deficiency. Decker (1947) has suggested that the vertical decrease in partial pressure of carbondioxide in the atmosphere, which drops from approximately 22.8mm at sea level to 13.0mm at 4572m higher, may be a critical factor limiting the upward extension of plants. However, this can hardly account for timberline, for research has not indicated that trees have higher requirements for carbondioxide than the shrubs and herbs which always

* For historical background, see Takahashi (1944).

extend higher. Furthermore, carbondioxide pressure varies directly with altitude, whereas timberline elevations vary greatly along both parallels and meridians. Although there can be but little doubt but that the usual carbondioxide deficiency becomes progressively greater with increase in altitude, this gradient cannot be related to the latitudinal and longitudinal gradients, or local variations, exhibited by timberlines.

Snow depth. Two biologists have concluded that the excessive depth and persistence of snow is a major factor determining upper timberline in the Selkirk Mountains of southeastern British Columbia (Shaw, 1909a) and in the Cascade Mountains of Washington (Taylor, 1923). These observers based their hypothesis principally on the fact that at high altitude in these mountains, tree seedlings cannot get established in depressions which accumulate snow early in autumn and retain it well into the next summer. Ridges that accumulate little or no snow cover support trees that are symmetrical, but have dead lower branches that suggest smothering by snow.

On both these mountain systems there are ridges that remain essentially free of snow but extend far above timberline, so the question of why trees do not follow the ridges farther upslope remains unanswered. It seems sufficient to consider snow accumulation as a factor controlling only the amount and distribution of trees in the levels just below tree line. Griggs (1938) has also expressed doubt as to the adequacy of this hypothesis on other grounds. Certainly if the evidence supporting the snow-depth hypothesis is not conclusive in those limited regions where snow-depth is recognized as above-average for alpine regions, it is even less adequate as an explanation of any of the major geographic trends under consideration.

Wind. In most extratropical parts of the northern hemisphere, trees at upper timberline are so dwarfed and wind-trained that ecologists have long had before them the hypothesis that wind sets the upper limits of trees on mountains. This hypothesis seems well supported by interpretations of phenomena to be observed widely at upper timberline north of the Tropic of Cancer. (1) The trees are asymmetrically deformed, the direction of asymmetry being consistent among individuals so as to suggest the influence of strong winds from a constant direction. (2) Projecting twigs frequently show the effects of fatal winter-desiccation, and the net effect of

this is to maintain smoothly contoured canopies surfaced with compactly crowded laterals, a new whorl of which is sent out each time the terminal is winter-killed (Shaw, 1909b). (3) The last trees up-slope are situated in depressions or equivalent microhabitats which offer a measure of protection from wind (Sochava, 1944; Daubenmire, 1943; Griggs, 1938, 1946). (4) Timberline may extend as much as 518m higher on the leeward slope of mountains in comparison with windward slopes (Schröter, 1926). (5) Timberline conditions may be reproduced locally on exposed knobs, shoulders, or passes far below the average elevation of upper timberline, and tends to rise and fall paralleling the contour of a ridge situated at right angles to the wind (Schröter, 1926; Antevs, 1932).

Within the tropics and beyond in the southern hemisphere these phenomena seem to be largely absent. The evergreen trees are commonly stunted and produce dense canopy-shells, but no other feature of the trees or their distribution suggests that wind is critical in these latitudes (Troll, 1948; for apparently local indications of wind importance, see: Haumann, 1918; Miller, 1918, p. 59; Lejungner, 1939).

In addition to the evidence afforded by the morphology and distribution of trees in the northern regions, climatic data (Table 1) show a pronounced vertical increase in winter wind velocities on mountain slopes. Bates' results (1924) are notable for the fact that just five hundred feet below timberline measurements of wind velocities were less than half the velocities at timberline. He was so impressed by this comparison that he stated: "There is no doubt in the mind of the writer that here (southern Colorado) the upper limit of timber growth is set by the mechanical effects of the wind and only indirectly by temperature conditions." A study in Italy that may be pertinent here showed the existence of a rather sharp increase in wind velocity at an altitude of 1800m, in a region where the land surface was 272m (Humphreys, 1916).

Despite the fact that wind data are very strongly influenced by the topographic setting of the measuring site, by the elevation of the anemometer above the ground, and by the nearness of trees, the meager data available appear to be adequate to draw certain conclusions. In Table 1 the stations are arranged according to their phytogeographic position with respect to upper timberline. The timberline elevations used in this case are intended as averages for the re-

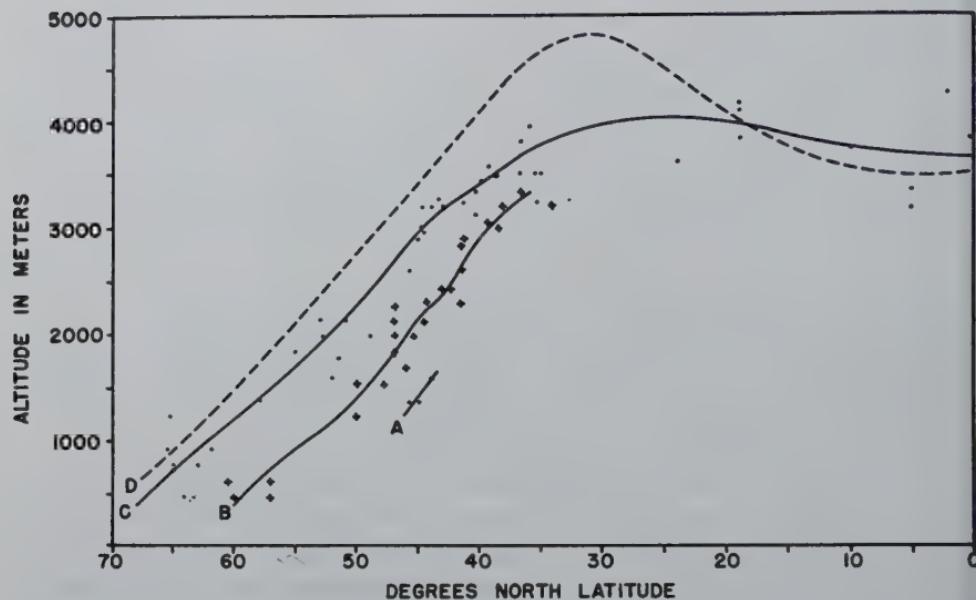


Fig. 1

gion as a whole as interpolated from curves A, B, and C in Figure 1. For the purpose of this comparison, the use of average rather than actual timberlines seems desirable because (1) in most cases specific data for timberline elevations at the weather station are unavailable, or sources differ in their estimates, so that reference to smoothed curves makes for uniformity in comparison, and (2) some weather stations are located on windy knolls and others in protected valleys so that timberlines at their locations may be abnormally lowered or raised by wind or heat influence. Another deficiency of the method lies in the fact that some of the records, which have been compiled from diverse sources, represent only a few seasons' observations. The winter velocity records for alpine tundra are impressive, but a most significant series of data are provided for Sandberg, California, which shows even higher values than on high mountains such as Pike's Peak. Sandberg is situated on a relatively low knob surrounded by chaparral with scattered pines, therefore far below upper timberline, but with the anemometer 30 feet above the ground. The conclusion seems inevitable that wind alone cannot explain the elevation of upper timberline. It may cause a local thinning of the forest, and intensify adversity imposed by other factors so that tree form and distribution are conspicuously influenced, but at least the mean wind

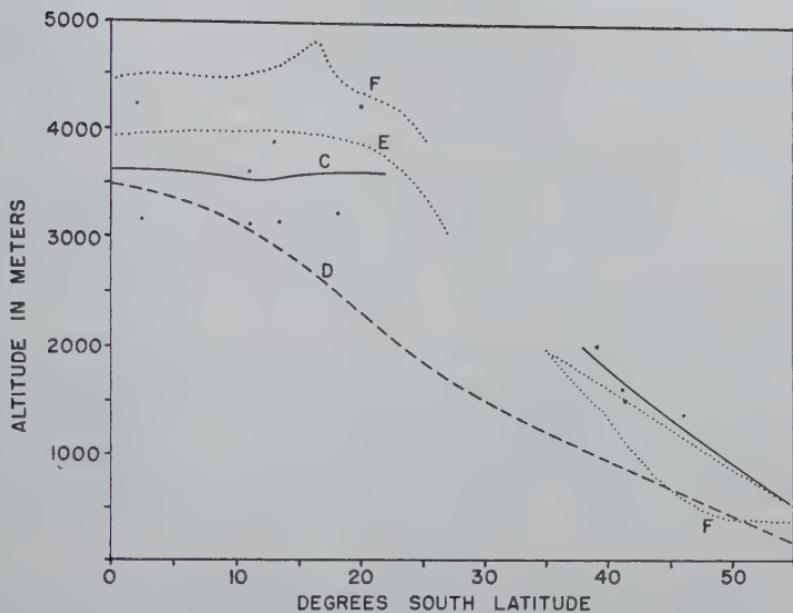


Fig. 2

velocity has no independent value in this problem of etiologic plant geography. Possibly with temperature decreasing upward at the same time wind increases, a critical ecologic sum may be quickly reached and exceeded that explains the relatively abrupt change from forest to tundra. However, a concept that cold soil may aggravate transpiration stress finds no support in observations by Polunin (1933) that tree roots at arctic timberline readily conduct water while imbedded in frozen soil. Also there are localities with timberlines conforming to the continental elevation-pattern as figured above, but where there is no asymmetry of the last trees which is essential for the hypothesis of wind control (Daubenmire, 1953). Finally, it may be pointed out that there is a tacit assumption by advocates of this hypothesis that the wind influences that so strongly modify the appearance and distribution of old trees is lethal to seedlings, but almost no direct evidence has been presented (Griggs, 1938, p. 559).

Desiccation during temperature inversions in winter. Studies of vertical stratification of the atmosphere in relation to alpine timberline in Europe have uncovered an interesting ecologic phenomenon which may prove to exist over wide enough area to have a bearing on the present problems. Michaelis (1932) has presented data show-

ing that the upper surface of a cool humid cloud layer coincides with upper timberline in central Europe. Immediately above this cloud layer bright insolation, high air temperature, low relative humidity, and scanty snow cover all conspire to increase transpiration stress at a season when the soil is cold and absorption may be sluggish. Such conditions are stated as being frequent in central Europe, but the degree to which they are attained elsewhere is unknown, and the meteorologic phenomenon has not yet been related to autecology in a convincing fashion.

Heat deficiency. A very old theory on the cause of arctic and alpine timberline is that it represents a point on the scale of diminishing heat beyond which this form of energy is inadequate to meet anabolic requirements. This theory is supported by two types of evidence.

The distributional peculiarities of trees growing at timberline on Mt. Shasta in the southern Cascades was interpreted by Merriam (1899) as indicating heat to be the most critical deficiency. At timberline on this mountain, trees are confined to ridgetops, from which they extend a short distance down only those slopes that face west. Merriam pointed out that such ridgeline habitats receive more insolation than the valleys between, and that west-facing slopes attain high temperatures because they are subject to insolation at the time of day when the air is warmest. Although this feature of timberline is well marked on Shasta, and the interpretation apparently warranted, the same feature of timberline is not generally characteristic of other mountains in the Americas. It is pertinent in connection with earlier discussion to note that all trees at timberline on Shasta are prostrate wind-cripples but are confined to the habitats most fully exposed to wind.

The second type of evidence for the heat hypothesis is indirect: the relation between isotherms and variations in the altitude or latitude of timberlines. The earliest quantitative work on this problem in the 19th century suggested that the climatic limits of cold timberlines coincide roughly with isotherms representing 10°C for the mean temperature of the warmest month. In 1903 de Quervain (see Schröter, 1926) showed that daily maximal temperatures in summer provide monthly means that are even more closely associated with the position of cold timberlines, and Brockmann-Jerosch in an ex-

tensive monograph (1918) verified this contention with data drawn from wide geographic area.

Owing to traditional methods of presenting weather data by the U. S. Weather Bureau, emphasis is placed upon averages of the daily maximal and minimal temperatures, with a result that the botanically important maximal values are so quickly buried as to be not readily available. If it may be assumed that the mean temperatures of the warmest months are a reasonable approximation, even if definitely inferior, of climatic differences that would be indicated by the maxima alone, the data from high mountain stations that are assembled in Table 2 are significant. Despite shortcomings of the data, as pointed out above, the fact is clearly established that the temperature of the warmest month is closely related to the position of the station with reference to timberline, whereas the actual elevation of the stations and of the timberlines show no relationship. Since the data show remarkable homogeneity despite their divergent latitudinal and longitudinal origins, and the shortness of the record in most cases, one must conclude that there is high probability of heat being critical or at least being closely related to a critical factor of wide importance for upper timberline.

Still another correlation between climatic records and timberlines is provided by a comparison of the curve B in Figures 1 and 2 with curves published elsewhere showing the latitudinal variations in elevation of isotherms representing mean annual temperature. Below an altitude of 8 km there is pronounced rise in altitude of all isothermal curves from north polar regions to about 24-14°N latitude according to Clayton (1923) or 30-20°N latitude according to Humphrey (1929), with a slight decline further southward to the equator. The curves for the southern hemisphere are essentially mirror images of these. Thus the temperature curves for latitude and altitude closely parallel the timberline curves for altitude and latitude.

The temperature and timberline curves described immediately above bear an interesting relationship to the air-mass source regions. Between 0-30° is the maritime-tropical air-mass source region which is characterized by relative homogeneity. This latitudinal belt corresponds closely with that part of the alpine timberline curve which is essentially horizontal. From 30-60°N latitude is a transition zone in which the maritime-tropical and the continental-polar influences

alternate in summer and winter respectively. Above 60° falls entirely within the continental-polar air-mass source region. It is obvious that the latitudes covered by the continental-polar air mass, even if only in winter, are characterized by a strong and uniform N-S cant in the alpine timberline curve. This correlation, if it may be assumed to have any direct significance, suggests that the intensity or duration of winter conditions controls timberlines, for the break in the timberline curve coincides with the southern extremity of the air-mass transition zone, and the continental-polar influence extends this far south only in the cold season.

Jensen (1949) has attempted an autecologic interpretation of timberlines. He points out that trees have the life form with the largest unproductive, but matter-consuming mass (i.e., stem and root). Thus timberline is set at that point along the scale of diminishing heat where the total annual production of dry matter is balanced by carbon compounds needed for respiration plus the formation of new leaves, so that none is left over for wood accumulation. This hypothesis is not difficult to accept after one has closely examined trees more than a century old but with stems less than a meter in length and 2 cm in maximum diameter.

Although the evidence in support of the heat deficiency hypothesis is relatively strong, it must be pointed out that indirect information of this type is only suggestive of likely points of attack for experimental work in fundamental autecology. The temperature hypothesis must undoubtedly comprise a significant part of the final explanation for timberline positions, yet it cannot furnish the sole basis of explanation. Locally the details of tree distribution (as described earlier) show far more correlation with wind exposure than with altitude which varies rather directly with temperature. The fact that in the Rockies the largest trees of timberline species are found just below timberline, whereas in the Appalachians trees are gradually reduced in stature over nearly a thousand feet of altitude (Antevs, 1932), suggests that if different factors are not concerned in these two regions, at least different emphasis need be placed on the constituents of the same factor-complex.

Light deficiency. Since ultra-violet, light and heat energy are all derived from solar radiation, it is difficult to isolate these factors to study their separate influences, although this is desirable from the

physiologic standpoint. It is, therefore, not unnatural for the hypothesis to have been advanced that light deficiency, resulting from the upward increase in cloudiness in certain mountain regions, may be critical in setting the altitude of upper timberlines. Kolaevsky (1939) assumes that precipitation varies somewhat directly with cloudiness, then he uses the more abundant precipitation data to test his hypothesis that light deficiency plus heat deficiency are critical. His studies in Eurasia tended to confirm the hypothesis, and Zotov (1938) reached the same conclusion from studies in New Zealand.

In North America, precipitation during the main season of vegetative activity, at least, is unrelated to timberline altitudes, according to the compilations in Table 2. Since, on the other hand, the heat supply, as indicated by temperature measurements, bear a close relationship, the heat form of energy appears the more important. But it is to be noted that the superiority of the heat hypothesis rests in part upon the assumption that light variation is adequately estimated from precipitation data.

SOME CONCLUDING REMARKS

Whatever the causal factor-complex that determines the position of climatically determined alpine timberlines, it is one which affects tall and low plants differently, for at the alpine timberline trees are generally reduced in stature, but the limitation does not prevent shrubs and herbs from extending much farther upward. In other words, the critical intensities of the atmospheric complex do not extend all the way down to the ground surface. It is to be noted that alpine herbs and shrubs have life-forms that enable them to take advantage of the warm layer of air near the ground, and that tree taxa which are capable of producing shrubby ecophenes often form a broad belt of scrub that extend well above those individuals exhibiting the tree form.

On a broad scale temperature and biologic data are so consistently related that some aspect of the temperature factor must be accorded high importance in any adequate explanation of alpine timberlines. On a small scale the temperature-determined timberline may be lowered in extratropical regions by strong winds or later-persisting snow cover, to elevations somewhat lower than a position which temperature would more directly set. But despite the striking effects

of wind and snow in such places, their influence upon timberline elevations is too small to disrupt the pattern of gradual change in elevation across a wide range of latitude. Thus the regions where timberlines give the appearance of being wind-induced or snow-induced alternate without causing recognizable modifications in the configuration of curves representing all mountain systems of North and South America.

It is possible that the increasing emphasis on high altitude meteorology in connection with aviation will result in the accumulation of data which will throw more light on the timberline phenomenon. Yet past experience has shown that those aspects of weather which attract attention from the professional meteorologist are not necessarily those which are biologically critical. In the last analysis the ecologist will have to resort to direct experimentation in the field and collecting his own environmental data to make a significant physiologic evaluation of the complex of factors that vary with altitude.

SUMMARY

Along the main axis of the North American Cordillera, the elevation of alpine timberline rises steadily at a rate of about 110m per degree of latitude between about 60 and 30°, then declines very gradually to the equator. In those latitudes where comparison is possible, alpine timberline is lower in the mountains near the Pacific Ocean and still lower in the Appalachians, but the rate of change along each axis appears identical.

The graminoid vegetation of the mountain summits of the southern Appalachians is only analogous with the usual alpine timberline, appearing to owe its existence to aridity resulting from peculiar air-mass phenomena.

In South America there is a similar cant in timberline elevations, but the point of flexure in the curve is closer to the equator (ca. 25°) and the relative height of timberline near and remote from the Pacific is reversed in temperate and tropical latitudes.

Because a great many genetically distinct trees contribute different segments of a timberline pattern that has remarkable geographic conformity, the hypothesis is suggested that a major autecologic principle is involved that may be analogous to the wilting co-

efficient of the soil, in which some environmental complex abruptly exceeds the tolerance of all trees regardless of variation among them.

The factor-complex is one that operates directly upon the tree life form, for shrubs and herbs extend well above timberline. From this it may be inferred that the critical conditions do not extend quite down to the soil surface.

The most promising autecologic theory to explain timberline is that it represents a point on the scale of diminishing heat supply where solar energy is adequate only to meet the annual requirements for respiration plus the requirement for foliage renewal, with a result that none is left to permit the development and maintenance of a large mass of non-productive cells as comprise the stem and root system of a normal tree. Evidence in favor of the heat-deficiency hypothesis is provided by (1) certain regions where the highest trees are on the best insulated habitats, (2) the conformity of timberlines to isotherms representing the mean of the daily maximal air temperatures of the warmest month, (3) the conformity of the north-south configuration of the timberline curves to the altitude of isotherms, and (4) the known fact that temperatures are higher in the layer of air near the ground, to which trees often become confined at their upper limits and in which shrubs and herbs extend far above timberline.

Winter winds and later-persisting snow may locally alter the appearance and elevation of timberline in extratropical parts of the northern hemisphere, but these influences never have enough significance to disrupt the general conformity between timberlines and isotherms. Hypotheses suggesting the importance of ultra-violet, of light, of carbondioxide deficiency, and of desiccation during temperature inversions in winter all appear to offer little in explaining the position of alpine timberlines.

TABLE I

Wind velocity in relation to mean timberline elevation in the U. S. A.

Station	Elevation in Meters Above Sea Level	In Rel. to Timberline	Mean Wind Velocity as Miles per Hour of Most Windy Month
Pike's Peak, Colorado	4334	+800	25.0
Mt. Washington, New Hampshire	1910	+400	42.5
Boulder County, Colorado	3750	+350	16.5
Pike's Peak, Colorado	3505 ¹	+100	20.8
Pike's Peak, Colorado	3455 ²	— 50	7.6
Boulder County, Colorado	3050	—350	13.4
Sandberg, California	1378 ³	—1870	21.1

¹ Instrument 3m above ground.² Instrument 6m above ground.³ Instrument 9m above ground.

TABLE II

Climatic data in relation to mean timberline elevation at different latitudes in the U. S. A. and Canada.

Station	Elevation in Meters		Mean Temp. of Warmest Month in °C.	Mean Monthly Precipitation in Inches				
	Above Sea Level	In Rel. to Timber- line		May	June	July	Aug.	Sept.
Pike's Peak, Colorado	4334	+800	5.1	—	—	—	—	—
Mt. Washington, New Hampshire	1910	+400	8.9	5.72	6.26	6.10	6.15	7.48
Alma, Colorado	3118	+300	10.2	1.48	0.68	2.85	2.63	0.86
Corona, Colorado	3555	+300	9.3	4.57	1.63	2.64	2.24	2.20
Pike's Peak, Colorado	3506	+100	10.8	—	—	—	—	—
Old Glory Mtn., Brit. Col.	2348	0	9.1	1.29	3.85	1.90	1.55	1.99
Rainier Paradise, Wash.	1693	—100	12.2	4.78	3.95	1.53	2.87	5.78
San Francisco Peak, Arizona	3506	—200	10.3	—	—	—	—	—
Wasatch Plateau, Utah	3079	—300	13.0	2.04	0.67	1.87	1.71	1.34
Crater Lake Head- quarters, Oregon	1969	—300	13.6	2.79	2.70	0.84	0.57	2.23
Lake Moraine, Colorado	3130	—300	12.0	2.91	2.53	4.30	3.89	1.68
Foxpark, Wyoming	2762	—500	12.0	1.65	1.45	1.70	1.39	1.48
Mullen Pass, Idaho	1835	—800	15.4	2.28	2.89	1.06	0.85	2.31
Hebgen Dam, Montana	1997	—900	15.0	2.24	2.10	1.80	1.38	1.68

LITERATURE CITED

ANTEVS, E. 1932. Alpine zone of the Mt. Washington Range. Pp. 118. Publ. by the author at Auburn, Maine.

BATES, C. G. 1924. Forest types in the central Rocky Mountains as affected by climate and soil. U.S.D.A. Bul. 1233. Pp. 152.

BRAUN-BLANQUET, J. 1951. *Pflanzensoziologie*. Pp. 631. Springer-Verlag; Vienna, Austria.

BROCKMANN-JEROSCH, H. 1918. Baumgrenze und Klimacharakter. Ber. Schweiz. Bot. Ges. 26. Pflanzengeogr. Kommission, Beitr. geogot. Landesaufnahme 6. Pp. 255. Rascher & Co.; Zuerich, Switzerland. (See *Journ. Ecol.* 8:63.)

CLAYTON, H. H. 1923. World weather. Macmillan Co.; New York. Pp. 393 (see p. 11).

COLLAER, P. 1943, 1940. Le role de la lumiere dans l'establissement de la limite superieure des forets. Ber. Schweiz. Bot. Ges. 43: 90-125; 50: 500-516.

— 1941. Le role de la lumiere dans l'assimilation chlorophyllienne. III. Ber. Schweiz. Bot. Ges. 51: 348-362. (See *Biol. Abstr.* 24-16759.)

DAUBENMIRE, R. 1943. Vegetation zonation in the Rocky Mountains. *Bot. Rev.* 9: 325-393.

— 1953. Notes on the vegetation of forested regions of the far northern Rockies and Alaska. *Northw. Sci.* 27: 125-138.

DECKER, J. P. 1947. The effect of air supply on apparent photosynthesis. *Plant Physiol.* 22: 561-571.

DONLEY, D. E. AND R. L. MITCHELL. 1939. The relation of rainfall to elevation in the southern Appalachian Region. *Amer. Geophys. Union Trans.* 1939: 711-721.

GANNETT, H. 1899. The timber-line. *Amer. Geog. Soc. Journ.* 31: 118-122.

GRIGGS, R. F. 1938. Timberlines in the northern Rocky Mountains. *Ecol.* 19: 548-564.

— 1946. The timberlines of North America and their interpretation. *Ecol.* 27: 275-289.

HAUMANN, L. 1918. (See *Geogr. Journ.* 67: 325.)

HERZOG, T. 1931. Baum- (Wald-) und Schneegrenzen in den Kordilleren von Suedamerika. *Mitt. Geogr. Gesellsch.* Jena 39: 72-89.

HUMPHREYS, W. J. 1916. Wind velocity and elevation. *Mo. Wea. Rev.* 44: 14-17.

— 1929. Physics of the air. 2nd ed., pp. 654. McGraw-Hill Book Co.; New York.

HUSTICH, I. 1952. (The polar limits of coniferous species) *Commun. Inst. Forest. Fenn.* 40(29): 1-20.

— 1954. On forests and tree growth in the Knob Lake area, Quebec- Labrador Peninsula. *Acta Geogr.* 13: 1-60.

JENSEN, P. BOYSEN- 1949. Causal plant-geography. *Biol. Meddel.* 21(3): 1-19.

KOLAEVSKY, G. V. 1939. (An experiment in the classification of mountain climates.) *Meteorol. i Hydrol.* 1939:83-87. (See *Biol. Abstr.* 16-14176.)

LEJUNGRER, E. 1939. A forest section through the Andes of northern Patagonia *Svensk. Bot. Tidskr.* 33: 321-337.

MERRIAM, C. H. 1899. Results of a biological survey of Mt. Shasta, California. U.S.D.A., Div. Biol. Surv., N. A. Fauna 16. Pp. 179.

MICHAELIS, P. 1932. Oekologische Studien an der alpinen Baumgrenze. *Ber. Deutsch. Bot. Ges.* 50: 31-42.

MILLER, L. A. 1918. In the wilds of South America. Pp. 424. Chas. Scribner's Sons; New York.

POLUNIN, N. 1933. Conduction through roots in frozen soil. *Nature* 132: 313-314.

SCHRÖTER, C. 1926. Das Pflanzenleben der Alpen. Pp. 1288. Raustein; Zuerich, Switzerland.

SHAW, C. H. 1909a. The causes of timberline on mountains; The role of snow. *Plant World* 12: 169-181.

——— 1909b. Vegetation and altitude. *Amer. Nat.* 43: 420-431.

SMILEY, F. J. 1921. A report upon the boreal flora of the Sierra Nevada of California. *Univ. Cal. Publ. Bot.* 9: 1-423.

SOCHAVA, V. B. 1944. (Causes of the treeless condition of mountains of eastern Siberia and the Amur region.) *Priroda* 33: 63-65. (See For. Abstr. 7-427.)

TAKAHASHI, K. 1944. Die Baum- und Waldgrenze in Hida-Gebirge (Japanische Nordalpen). Ein Beitrag zur Baum- und Waldgrenze ostasiens. *Jap. Journ. Bot.* 13: 269-343.

TAYLOR, W. P. 1923. A distributional and ecological study of Mt. Rainier, Washington. *Ecol.* 3: 214-237.

TROLL, C. 1948. Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord- und Suedhalbkugel. *Ber. Geobot. Forsch.* Ruebel 1947: 46-83.

U.S.D.A. 1941. Climate and man. Pp. 1248. U. S. Govt. Print. Off.; Wash., D. C.

ZOTOV, V. D. 1938. Some correlations between vegetation and climate in New Zealand. *N. Z. Journ. Sci. Techn.* 19: 474.

HEPATICAEE FROM THE FEDERAL DISTRICT, MEXICO. I.*

By DOROTHY PARKER†

Although the Hepaticae are well represented in the flora of Mexico very few reports concerning them have been published. The scarcity of keys to the species, the difficulty in obtaining authentic specimens of the species that were described in early European publications, and the great variation in size and form of many of the species that have been collected make their classification difficult.

The liverworts reported below were collected in the Federal District which is located in the center of Mexico in the Central High Plateau, surrounded by the state of Mexico on the west, north and east, and by the state of Morelos on the south. The District occupies a segment of approximately 573 square miles that is irregular in shape located on the southwestern part of the Valley of Mexico and includes terrain which extends from the bed of the lakes on the valley floor to the heights of the surrounding mountains in the Sierra de Ajusco. The elevations range from 7,000 to more than 12,000 feet. A series of small streams drain the area, the majority of which are temporary. The drainage leads to canals of the series of lakes in the valley.

The climate is considered as subtropical of a high elevation type, however, considerable variation is encountered. Mexico City occupies much of the lower elevations in the area between 7,000 and 7,500 ft. and is semi dry with approximately 30 inches of rainfall during the months of May to October. The winter and spring are generally dry. At higher elevations there is heavier precipitation and lower winter temperatures. Meteorological data from the Desierto de los Leones at 9,660 ft. record an annual rainfall of approximately 50 inches. At this elevation and higher a dry, cold, definite winter season occurs.

In the lower part of the District the vegetation has been almost completely destroyed by the growth of the capital. Above the city

* The writer is indebted to Dr. Margaret Fulford, University of Cincinnati, Cincinnati, O., for verifications and corrections of the species reported.

† The Rockefeller Foundation, Mexico, D. F.

remnants of the pine-oak forest can be found above which is a wide belt of religious fir forest that has been protected in a National Forest area.

In spite of the heavy population in the Federal District (more than 3,000,000 according to the 1950 census) a surprisingly rich flora still exists. This report is the first of a series that has been started with the hope that over a period of years more information concerning the members and distribution of the Hepaticae of this area will result. All of the following were collected along the banks of a small stream in a protected ravine of the fir forest above the town of Contreras, D. F. The numbers following each species refer to the collection numbers of the writer.

Targioniaceae

Targionia hypophylla L. 701, 738

Rebouliaceae

Reboulia hemisphaerica (L.) Raddi 731

Asterella sp? 708

Marchantiaceae

Marchantia polymorpha L. 704, 739, 740

Riccardiaceae

Metzgeria conjugata Lindb. 709, 720, 726

Metzgeria furcata (L.) Dum. 707, 709, 719, 724

Metzgeria hamata Lindb. 727

Metzgeria Liebmanniana L. & G. 711, 719, 732

Metzgeria uncigera Evans 725

Metzgeria sp? 721, 728

Riccardia sp? 717, 718

Lophoziaaceae

Lophocolea bidentata (L.) Dum. 702, 703, 712, 713, 727, 736, 737

Lophocolea sp? 722, 723

Plagiochila sp? 720, 721, 735

Porellaceae

Porella platyphylla (L.) Lindb. 710, 720

Lejeuneaceae

Dicranolejeunea incongrua (L. & G.) St. 716

Microlejeunea sp? 714, 715

Strepsilejeunea sp? 734

Anthocerotaceae

Anthoceros sp? 705, 729, 733

PRESERVATION OF SOME ALGAL CULTURES BY LYOPHILIZATION

By W. A. DAILY AND J. M. McGuire

The Lilly Research Laboratories, Eli Lilly and Company
Indianapolis, Indiana

Lyophilization has come to be widely used as a means of maintaining viable cultures of microorganisms in a desiccated state. Experimental application of this method of preservation in the algal group was therefore undertaken.

Raper and Alexander (1) believe that morphological and physiological characteristics of some of the fungi are not altered by such treatment. In their hands, strains of *Penicillium notatum* and *P. chrysogenum* preserved by lyophilization retained their original capacities to produce penicillin. Insofar as the algae cited in this paper are concerned, microscopic examination of the cells in viability check cultures indicated no morphological differences from the original cultures.

All but two of the cultures were supplied by Dr. Richard C. Starr of Indiana University. The Indiana collection number is affixed to each species.

CULTURE METHODS

The algae noted herein were cultivated on modified Chu No. 10 medium (2). The composition of the nutrient in grams per liter was as follows: NaNO_3 , 0.124; $\text{K}_2\text{HPO}_4 \cdot 3\text{H}_2\text{O}$, 0.013; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.025; Na_2CO_3 , 0.020; $\text{Na}_2\text{SiO}_3 \cdot 9\text{H}_2\text{O}$, 0.058; $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$, 0.036; ferric citrate, 0.003; and citric acid, 0.003.

A temperature of 25°C was maintained and fluorescent tubes served as the light source.

LYOPHILIZING PROCEDURE

The algal suspensions were prepared by introducing 1 ml of sterile horse serum into the agar slant cultures. One tenth ml of each cell suspension was then dispensed into each of six sterile, cotton-plugged

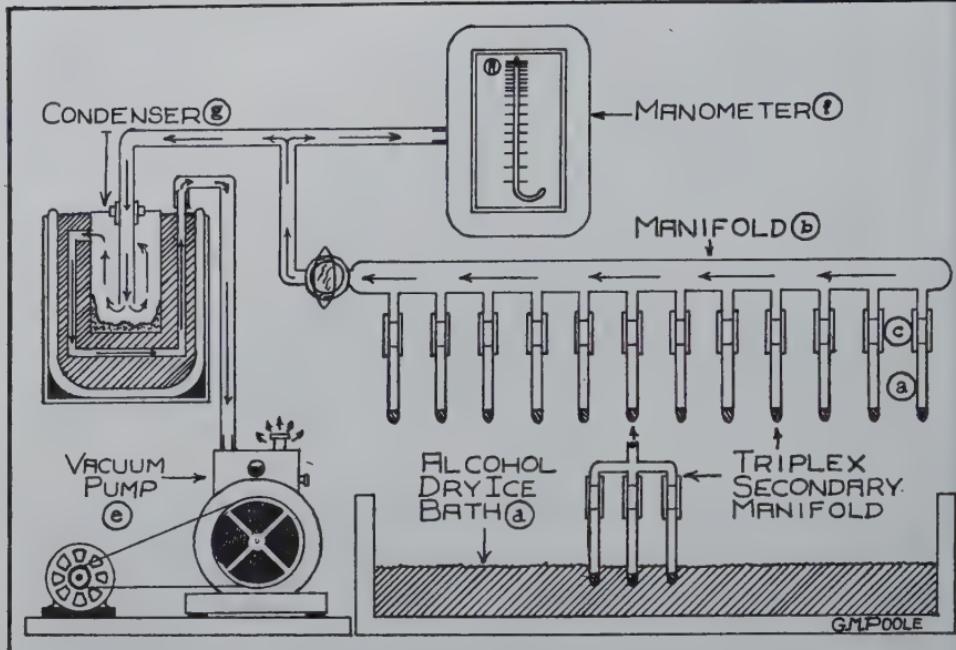


Fig. 1

(13 cm lengths of 7 mm Pyrex glass tubing, sealed at one end and lightly fire-polished at the lip) lyophil tubes by means of a sterile glass syringe fitted with a 9 cm 13 gauge syringe needle. The excess cotton on the plugs was burned off and the remainder pushed down into the tubes to a depth of about 1 cm as a precaution against possible contamination during processing.

The lyophil tubes (Fig. 1a) containing the algal suspensions were then attached to the manifold (Fig. 1b) of the lyophil apparatus by inserting them into the rubber sleeves (Fig. 1c). The manifold was then lowered into the bath (Fig. 1d) containing dry ice in ethyl cellosolve* until the bottoms of the tubes were submerged. The material in the tubes was completely frozen within a few seconds, and evacuation by means of vacuum pump (Fig. 1e) was begun immediately. After approximately two minutes (or until a minimum vacuum (Fig. 1f) of 150u of mercury is maintained) the temperature of the bath was raised from -55°C to -10°C . During the ensuing 1 1/2 hours, the temperature of the bath was allowed to rise slowly to about 0°C by which time chalky loose pellets were formed in the tubes. The moisture removed from the lyophil tubes is retained in

* Ethylene glycol monoethyl ether.

the condenser (Fig. 1g) where it collects as ice. The manifold was then raised from the bath and the vacuum was maintained for another hour at room temperature to insure thorough desiccation. The tubes were then sealed off *in vacuo* with a cross-fire gas-oxygen torch.

Within 24 hours or less after processing, the lyophil tubes were tested with a high-frequency, spark-coil tester to ascertain the existence of a vacuum.

Lyophilized cultures were checked for viability as follows. A lyophil tube was marked with a file scratch, swabbed with alcohol and broken open. The pellet was dissolved in sterile distilled water and the resulting suspension, appropriately diluted, was pipetted into agar plates and incubated for a period of 10 days, or until definite colonies developed.

No effort was made to modify any of the above processes, which are routinely employed for the preservation of other types of micro-organisms in the Lilly Research Laboratories. Modifications in procedure and suspending agent could possibly be developed which would allow successful preservation of algal cultures which did not survive the process described here.

ALGAL CULTURES LYOPHILIZED

Chlorophyta

- +8 *Bracteococcus cinnabarinus* (Kol. & F. Chodat) Starr #56
- *Carteria crucifera* Korsch #432
- +7 *Chlorella luteoviridis* Chodat var. *lutescens* Chodat #248
- *Chlamydomonas orbicularis* Pringsheim #218
- + *Chlamydomonas pseudococcum* Lucksch #214
- +10 *Chlorella protothecoides* Krüger #25
- *Chlorella vulgaris* Beijerinck #263
- +4 *Chlorella vulgaris* var. *viridis* Chodat #30
- *Chlorococcum macrostigmatum* Starr #109
- + *Coccomyxa elongata* Jaag #267
- *Cosmarium formulosum* Hoff #303
- *Haematococcus lacustris* (Girod.) Rostaf. #16
- +4 *Muriella aurantiaca* Vischer #36

- + *Prototheca chlorelloides* Krüger #178
- + *Prototheca moriformis* Krüger #288
- + *Prototheca portoricensis* Ciferri & Ashford #289
- +4 *Scenedesmus dimorphus* Kütz. #417
- +4 *Scenedesmus dispar* Bréb. #414
- +4 *Scenedesmus Naegeli* Chodat #74
- +7 *Scenedesmus obliquus* (Turp.) Krüger #78
- *Selenastrum minutum* (Naeg.) Collins #326
- + *Stichococcus bacillaris* Naeg. #419

13—BUTLER BOTANICAL STUDIES

Chrysophyta

- +4 *Polyedriella helvetica* Pascher #49
- +4 *Vischeria punctata* Vischer #153

Bacillariophyceae

- *Navicula minima* Grun. #391

Cyanophyta

- + *Lyngbya* sp. #487
- + *Lyngbya* sp. #488
- + *Lyngbya versicolor* (Wartm.) Gom. #29V Lilly
- + *Nostoc* sp. #387
- + *Nostoc* sp. #389
- + *Nostoc ellipsosporum* (Desmaz.) Rabenh. ex. B. & F. #27E Lilly
- + *Phormidium luridum* var. *olivace* Boresch #426

Legend:

- + = viable when tested within 24 hours following lyophilization.
- +8 = viable at least 8 months after lyophilization.
- = non-viable immediately after lyophilization.

RESULTS

From a total of 32 cultures lyophilized, 24(75%) were viable when tested within 24 hours following desiccation. These continue to be checked periodically for viability. Duplicate lyophil tubes were cultivated recently, at from 4 to 10 months after lyophilization and they were still viable.

No spores or resting cells were seen in any of the cultures.

The percentage of cells of three species remaining viable after drying, determined by plate colony counts before and after drying was as follows:

Culture Lyophilized	Pct. Survivals
<i>Scenedesmus obliquus</i>	0.025% viable cells
<i>Bracteococcus cinnabarinus</i>	3.166% " "
<i>Chlamydomonas pseudococcum</i> ..	0.013% " "

CONCLUSIONS

The percentage viability of algal cultures withstanding lyophilization compares favorably with that of other groups of microorganisms, viz., bacteria, actinomycetes and molds when dried by a similar procedure.

The percentage of algal cells in 3 cultures remaining viable after desiccation, compares favorably with some bacteria (3).

This study demonstrates the practicability of lyophilization of the algae as a method of preserving certain algal cultures. If all algal cultures to be lyophilized are in excellent vegetative or sporiferous condition, a higher percentage viability rate probably can be achieved.

ACKNOWLEDGMENTS

The authors express their sincere appreciation to George M. Poole of the Lilly Research Laboratories for valuable technical assistance.

LITERATURE CITED

1. RAPER, K. B. AND ALEXANDER, D. F. Preservation of Molds by the Lyophil Process. *Mycologia* 37: 4: 499-525. 1945.
2. GERLOFF, G. C., FITZGERALD, G. P. AND SKOOG, F. The Isolation, Purification and Culture of Blue-Green Algae. *Amer. Jour. Bot.* 37: 216. 1950.
3. HORNIBROOK, J. W. A simple, inexpensive apparatus for the desiccation of bacteria and other substances. *Jour. Lab. Clin. Med.* 34: 1315-1320. 1949.

A RARE TOLYPELLA NEW TO THE UNITED STATES OF AMERICA

By FAY KENOYER DAILY

In a small lake near Laramie, Wyoming, Dr. C. L. Porter of the University of Wyoming collected a variety of *Tolypella hispanica* Nordst., a rare dioecious species new to the United States of America. This is the only dioecious species of *Tolypella* reported so far, having been found in the north temperate region of Europe, Asia and North Africa.

The collection of *Tolypella hispanica* from Wyoming is considered sufficiently different from the holotype of the species and the var. *microcephala* to establish a new variety *Tolypella hispanica* var. *Porteri* named after Dr. C. L. Porter who found it. A characterization is given below:

Tolypella hispanica var. *Porteri* nov. var.

Plate I, Figs. 2-7; Plate II, Figs. 6-11

Varietas a typo potissimum habito miniore condenso; ultimis segmentis fertilium ramulorum usualiter inflatioribus ad basis; ultimis cellulis ultimorum segmentorum allantoideis sed brevioribus et cum miniore diametro; nucleis cum 5-6 prominentibus gyراتis, ca. 285-315 μ longis, ca. 210 μ crassis; antheridiis ad 1050 μ in diametro.

A variation from the type especially by the smaller, condensed habit; terminal rays of the fertile branchlets inflated at the bases; ultimate cells of the terminal rays allantoid but shorter and with smaller diameters; nuclei with 5-6 prominent spirals, about 285-315 μ long, about 210 μ wide; antheridia to 1050 μ in diameter.

A complementary diagnosis follows:

Dioecious. Male and female plants similar, variable, but male usually somewhat smaller and compact, up to 4 cm. in height. Stem ca. 633 μ in diameter. Fertile branchlets of varying size, once-divided with usually 3 lateral rays of ca. 3 cells and a terminal ray of ca. 3 cells. Sterile branchlets of varying size, simple, usually of ca. 3 or 4 cells. Oogonia clustered at the fundus of the verticil and

at the branchlet node, enveloping cells inflated at maturity. Coronulae of oogonia deciduous, upper cells 30 μ high, lower cells 20 μ . Oospores red-brown. Outer colored oospore membrane with scattered large granules up to 5 μ in diameter on a background of smaller granules, superficially spongy at maturity. Antheridia clustered at the fundus of the verticil and at the node of the fertile branchlet, stalked.

Type specimen: Wyoming: Albany County: Forming rounded, cushion-like tufts in ca. 2 ft. of alkaline water in a small lake, 7 miles southwest of Laramie, 7,200 ft. altitude, C. L. Porter 6191, Aug. 25, 1952. (In the Butler University Herbarium and a duplicate at the Rocky Mountain Mountain Herbarium, University of Wyoming).

The holotype of *Tolypella hispanica* Nordst. (Plate I, Figs. 8-11; Plate II, Figs. 2-5) collected by Nilsson (No. 27) in Spain may not be as mature as the Porter collection as the oospores are much more difficult to dissect from the enveloping cells. The oospores are brown with the membrane showing little sponginess, and the oogonia show less inflation of the enveloping cells. These differences could be due to lack of maturity. Some plants attain 10 cm. in height although other plants are smaller than this approaching the stature of Var. *Porteri*. The branchlets are somewhat more uniform in size at a verticil. The ultimate rays of the branchlets taper more gradually to the tip. To some extent, there is less crowding and condensing of the verticils although some differences in these respects are seen among plants of the holotype.

Tolypella hispanica var. *microcephala* Nordst. (Plate I, Fig. 1) seems similar to the type except for the small fruiting heads, and larger oospores (oospores up to ca. 250 μ long in the type, but up to ca. 300 μ long in var. *microcephala*). The oospores in this variety do not seem to reach the size for var. *Porteri* and the antheridia are not as large. The inflation of the basal cell of the ultimate ray is not seen in this variety either, as it is in variety *Porteri*.

Further collection of this species will undoubtedly show much intergradation between the type and the varieties now established, if one can judge from the diversity of individuals within a collection and from the difference of branchlets in a single whorl. However, the establishment of var. *Porteri* seems justified at this time upon the basis of the above observations and according to the present knowledge and arrangement of the species.

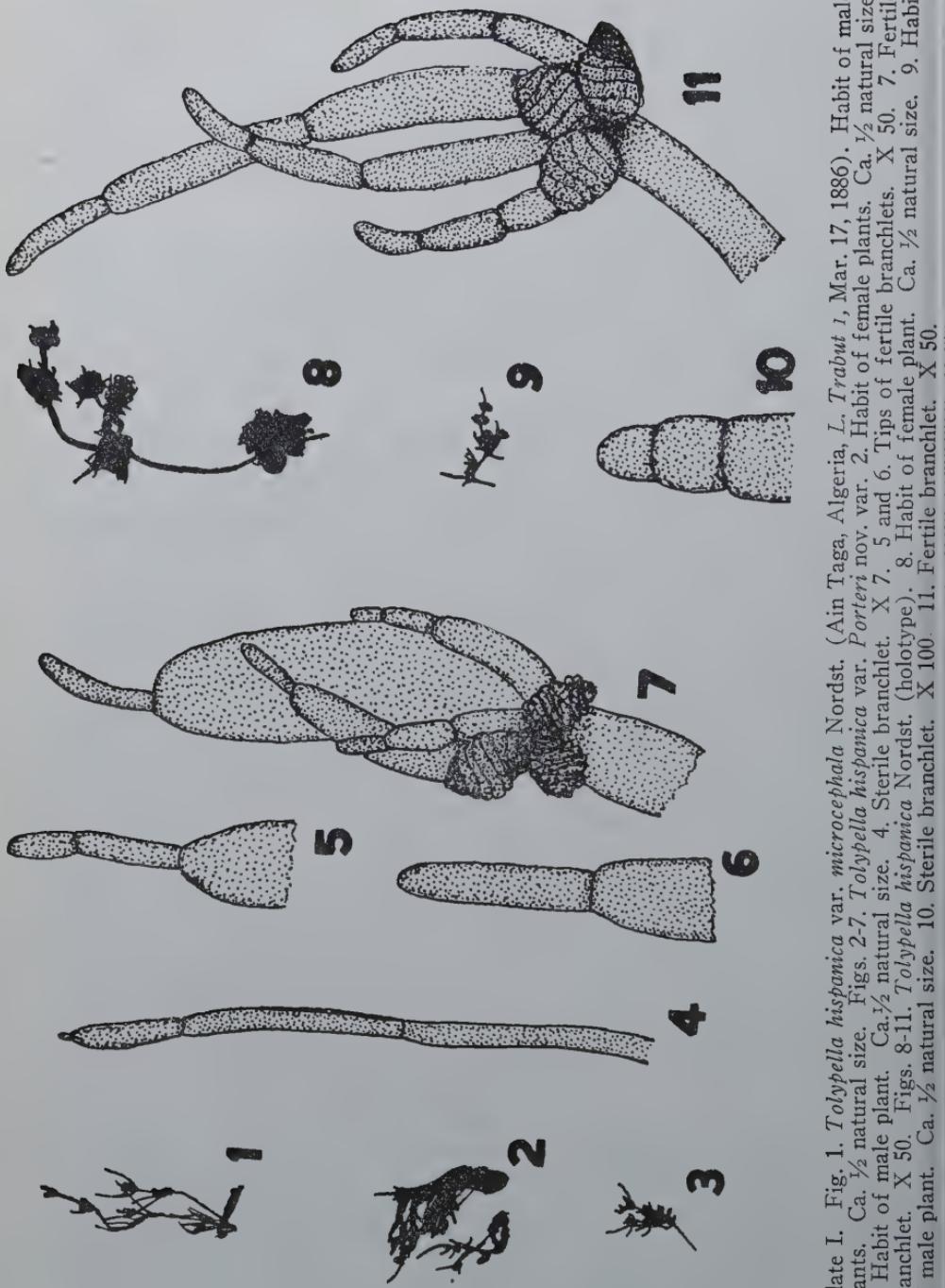


Plate I. Fig. 1. *Tolyella hispanica* var. *microcephala* Nordst. (Ain Taga, Algeria, L. Trabut 1, Mar. 17, 1886). Habit of male plants. Ca. $\frac{1}{2}$ natural size. Figs. 2-7. *Tolyella hispanica* var. *Porteri* nov. var. 2. Habit of female plants. Ca. $\frac{1}{2}$ natural size. 3. Habit of male plant. Ca. $\frac{1}{2}$ natural size. 4. Sterile branchlet. X 7. 5 and 6. Tips of fertile branchlets. X 50. 7. Fertile branchlet. X 50. Figs. 8-11. *Tolyella hispanica* Nordst. (holotype). 8. Habit of female plant. Ca. $\frac{1}{2}$ natural size. 9. Habit of male plant. Ca. $\frac{1}{2}$ natural size. 10. Sterile branchlet. X 100. 11. Fertile branchlet. X 50.

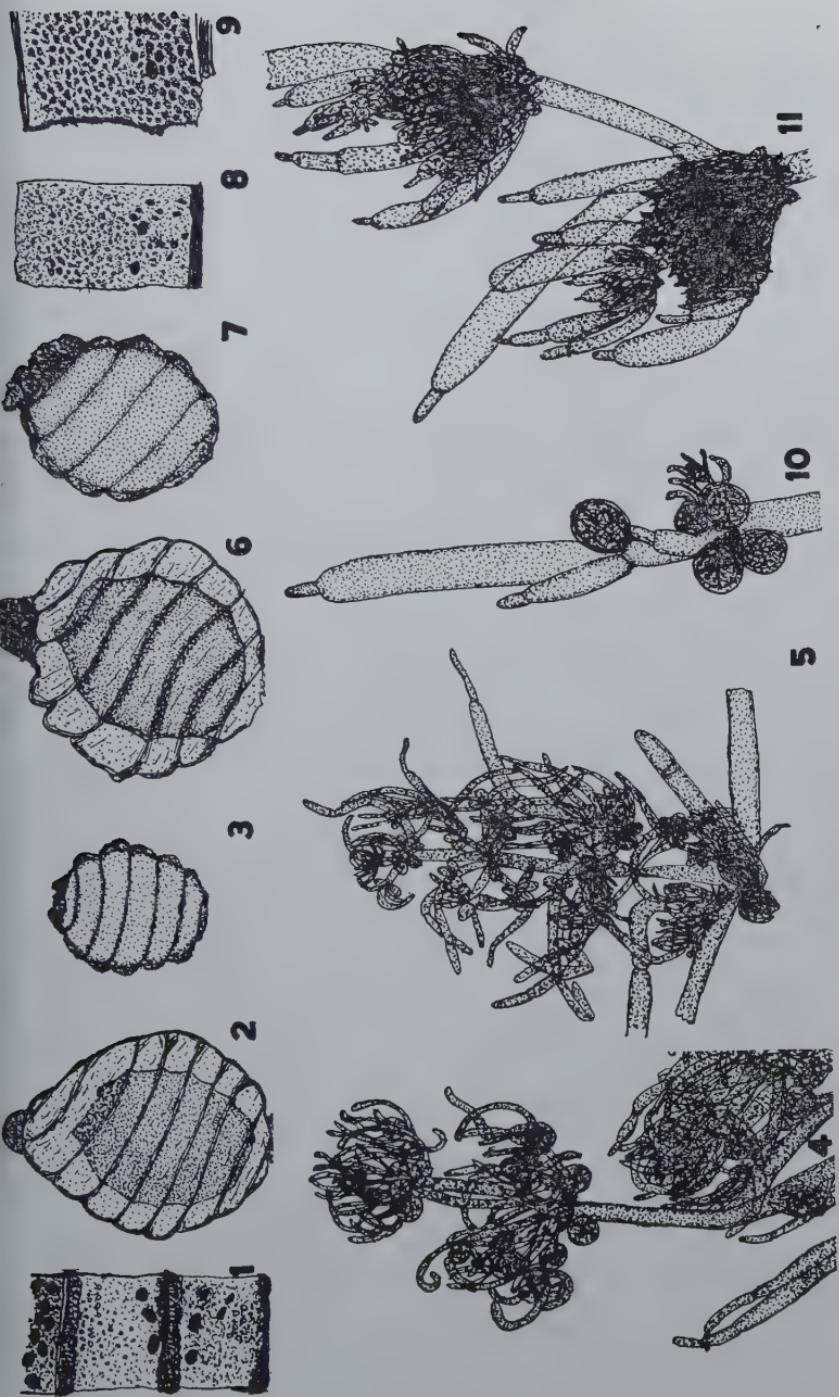


Plate II. Figs. 1-5. *Tolypella hispanica* Nordst. (holotype). Outer colored oospore membrane. Ca. X 430. 2. Oogonium. Ca. X 430. 3. Oospore. Ca. X 100. 4. Tip of male plant. Ca. X 7. 5. Tip of female plant. Ca. X 7. 6-11. *Tolypella hispanica* var. *Porteri* nov. var. 6. Oogonium. Ca. X 100. 7. Oospore. Ca. X 100. 8. Outer colored membrane of oospore. Early developmental stage. Ca. X 430. 9. Outer colored membrane of oospore. Mature stage. Ca. X 430. 10. Tip of male plant. Ca. X 7. 11. Upper portion of female plant. Ca. X 7.

ACKNOWLEDGMENTS

The author wishes to acknowledge the kind cooperation of Dr. C. L. Porter, the Rocky Mountain Herbarium, University of Wyoming, Laramie; Dr. Henning Horn af Rantzien, Riksmuseets, Stockholm, Sweden; Dr. Tycho Norlindh, Universitets Botaniska Museum, Lund, Sweden; and Dr. L. Faurel, Laboratoire de Botanique de la Faculte des Sciences, Universite de Alger, Algeria.

BIBLIOGRAPHY

ALLEN, T. F. The Characeae of America 1: 1-64. New York, 1888.

FELDMANN, GENEVIEVE. Les Charophyees d'Afrique du Nord. Bul. Soc. Hist. Nat. de l'Afrique du Nord 37 (1-9) : 64-74. 1946.

GROVES, J. Notes on the Indian Charophyta. Jour. Linn. Soc. Bot. London 46 (310) : 347-414. Apr. 16, 1924.

MIGULA, W. Die Characeen Deutschlands, Oesterreichs und der Schweiz. in Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz 5. Leipzig, 1897.

NORDSTEDT, OTTO. De Algis et Characeis 4. Uber die Hartschale der Characeenfruchte. Aft. af Lunds Univ. Arssk. 25: 2-17. 1889.

_____. De Algis et Characeis 5. Uber einige Characeen aus Spanien. Aft. af Lunds Univ. Arssk. 25: 17-22. 1889.

_____. De Algis et Characeis 6. Ueber einige extraeuropaische Characeen. Aft. af Lunds Univ. Arssk. 25: 22-42. 1889.

ZANEVELD, J. S. The Charophyta of Malaysia and Adjacent Countries. Blumea 4(1) : 1-224. 1940.

The Herbarium

Butler University

QUANTITATIVE RELATIONSHIPS OF TERRESTRIAL MOSSES WITH SOME CONIFEROUS FORESTS AT MT. RAINIER NATIONAL PARK

By N. HIGINBOTHAM AND BETTY WILSON HIGINBOTHAM

Relatively few studies have been made on the correlation of moss societies with tree species in climax associations in North America; this is true despite the fact that in Europe moss unions have been accorded considerable importance along with societies of larger plants in delimiting phytocoenoses. The present study is an attempt to characterize as accurately as possible the terrestrial moss communities of typical climax stands in a given area, largely in Mt. Rainier National Park, and to discover how closely related bryophyte occurrence, frequency, and coverage may be to the societies of higher plants.

The literature on bryo-sociology, as it may pertain here, has been summarized by Cain and Sharp (4) and therefore is not reviewed here. Cain and Penfound (3) included moss societies in their study of the *Acer rubrum* swamps of Long Island. In the most extensive moss ecology study in North America, Cain and Sharp (4) have described a number of moss communities found in forest types of the Great Smoky Mountains. In six forest associations 34 bryophyte communities were described on the basis of a systematic sampling method; the accuracy of the latter was tested by means of the species-area curve. They concluded that 23 of the 34 moss communities could be classified in 2 alliances comprising 10 unions and 14 (union) facies; the remaining moss communities were not so well characterized because they were less frequent or they appeared to be seral. In their study four substrate types were systematically estimated: terrestrial, epilithic, epixylic, and corticolous. It was noted that a number of species occurred in more than one habitat type and also that they ranged over two or more forest associations. Cain and Sharp emphasized species range in their discussion; however, their data show numerous correlations of the moss societies with the climax tree stands. The combinations of dominant bryophyte species seem to differ in each forest type, and some species, such as *Hypnum splendens*, were found to be essentially restricted to as-

sociations in which *Abies fraseri* and *Picea rubens* were dominant species.

Ilvessalo (8) has attempted to give some evaluation of forest (site) types in North America by use of the ground cover as indicators. Some moss species were found to be important in a number of stands. The stands he reported on were spread over widely differing climatic areas and data were given on groups of moss species; close correlations of mosses with tree communities, therefore, were not revealed in this work.

METHODS

Selection of individual stands to be studied was based on consideration of all the various forested zones of the eastern portion of Mt. Rainier National Park and on the criteria for climax stands as subjectively judged. A tree species was considered dominant when there was good evidence that it was maintaining itself as shown by reproduction and the presence of a range of sizes from seedlings to large trees competing for the overhead canopy. Stands in which mature tree species were not reproducing themselves were considered immature or seral; such stands typically showed a multiplicity of species uncharacteristic of older stabilized forest sites.

Estimates of mosses, shrubs, and herbs were made by use of Braun-Blanquet (1) coverage scale in 0.1 square meter plots (20 cm. x 50 cm.) distributed along a straight line. With some exceptions, which are noted below, the plots were taken at each meter (0.8-meter spacing), with 25 plots examined for each stand. The exact location of the line of plots was selected as that typical of undercover areas of the stand as a whole. In particular, mesic ground surface was chosen; streams, low wet spots, rock outcrops, and chance clusters of logs were avoided. However, every substrate occurring in the plots was included in the estimates, including logs, tree bases, and rock. It should be emphasized that, in general, this method leads to a measure of relatively mature vegetational areas and minimizes seral species.

Tree coverage estimates were made in essentially the same manner, but, of course, do not represent a similar accuracy. These estimates were intended to indicate primarily the direct overhead coverage of the small plots. The species are believed to be typical of the

climax stand in each case, although the figures as given may not accurately reflect the degree of coverage of each species.

Only five coverage classes were used here in contrast with the method used by Cain and Sharp, who used a sixth, x, to indicate occurrence of a species covering 1 per cent or less (of community area). Also, in the present work, coverage and frequency data are reported in percentages, as shown in table 1.

TABLE 1

Coverage classes and percentages used in estimating area of communities.

Class	Percentage coverage range	Value (percentage used in calculating average coverage)
1	0 - 5	2.5
2	5 - 25	17.5
3	25 - 50	37.5
4	50 - 75	62.5
5	75 - 100	87.5

DESCRIPTION OF AREA

The area under study lies largely in the eastern portion of Mt. Rainier National Park and consists of the eastern slopes of Mt. Rainier (at lower elevations) and the western slopes of the Cascade Mountain Range. Eleven of the stands were within the drainage system of the Ohanapecosh River, which originates from the Ohanapecosh Glacier. Since this area is west of the divide of the Cascade Range, it receives a relatively high amount of precipitation, particularly between October and May, with much of the precipitation as snow. No records are available for precipitation in the immediate vicinity of most of the stands; however, at Longmire (2,760 ft.) about 12 miles west of Ohanapecosh Hot Springs, the mean annual precipitation is given as 78 inches, and at Paradise Park (5,557 ft.), northwest of Ohanapecosh Hot Springs, as about 100 inches (2). Since high ridges and old mountain peaks lie between these locations and the Ohanapecosh River, it is possible that a somewhat lower precipitation occurs in the region of the stands studied.

MEASURE OF ACCURACY OF THE METHOD

A common method of determining the area size required for estimating the importance of species in a community is the species-area

curve. In the present study some test of the accuracy is given by the data from stand 10 in which 50 plots were taken and calculated cumulatively in groups of five as shown in table 2. The number of species becomes nearly constant in the first 15 plots; an additional 35 plots added only one more species. Of greater significance, probably, is the estimate of percentage area covered by a species. Only 5 plots would closely reflect the relative abundance of the two more important species. The decision to use 25 plots for a stand, in most cases, seems quite adequate for the purposes of this study. It should be pointed out, however, that in regions having a lesser moss cover and/or an uneven distribution, this number might not be adequate.

TABLE 2

The relation of area to number of bryophyte species and coverage. Area by cumulative 5-plot totals, 0.1-meter plots. Data from stand 10 (*Abies amabilis*-*Tsuga heterophylla* community).

Plots	1-5	1-10	1-15	1-20	1-25	1-30	1-35	1-40	1-45	1-50
No. species	3	4	6	6	6	7	7	7	7	7
Per cent coverage (total bryophytes)	58	58	54	58	61	59	54	51	55	52
Species coverage										
<i>Rhytidiodiopsis robusta</i>	36	44	40	43	47	45	42	40	42	39
<i>Dicranum fuscescens</i>	17	13	13	14	14	13	11	10	12	12
Other species	5	1	1	1	0	1	1	1	1	1

DESCRIPTION OF THE STANDS AND RESULTS

Pseudotsuga menziesii community

Two stands of forest which apparently represent a climax of *Pseudotsuga menziesii* (Douglas-fir) were studied. Stand 1 was located on State Route 5 at Summit Creek (1.5 miles south of the park boundary) and stand 2 was 2.0 miles south of Clearfork River (4.8 miles south of the park boundary). Approximate elevations of the study sites were 1800 and 1600 feet respectively.

In these forests almost pure stands of Douglas-fir were found with all stages of reproduction and trees ranging up to more than 3 feet DBH. Although *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western red cedar) occupy moister areas nearby, they did not appear to be invading the Douglas-fir stands. The more con-

spicuous plants associated with the Douglas-fir are *Acer circinatum*, the vine-maple, a shrub or small tree forming a scattered understory, and the low shrubs *Gaultheria shallon* and *Berberis nervosa*. Estimated coverage values for these and other species are given in table 3.

The mosses which were most abundant and frequent under Douglas-fir were *Eurhynchium oreganum*, *Hylocomium splendens*, and *Rhytidadelphus triquetrus*. The most striking feature here, perhaps, is the high frequency of *Eurhynchium oreganum* in the Douglas-fir community and the lesser frequency of this species in other sites (table 3). The frequency of *Eurhynchium oreganum* seems directly related to the coverage value of Douglas-fir in all stands. This feature plus the coverage of *Rhytidopsis robusta* under *Tsuga heterophylla* appears to delimit sharply the Douglas-fir stands from those of western hemlock.

Here, as in other stands, only 2 or 3 moss species contribute in a major way to the moss layer. Although other species could possibly be of value as indicators, they are not of significance in coverage or frequency.

Tsuga heterophylla-Thuja plicata community

In certain areas, at the level of the Douglas-fir stands and above, forests were observed to be predominantly of *Tsuga heterophylla* with *Thuja plicata* occupying more moist portions of lower topography (e.g., temporary stream channels). The zone of western hemlock predominance extends upward to regions occupied primarily by *Abies amabilis*, the Pacific silver fir, at elevations beginning at 2000 to 2700 feet; here *Abies amabilis* forms climax stands with western hemlock and western red cedar as lesser but codominant species. The *Tsuga heterophylla-Thuja plicata* community thus occupies much of the area between 1600 and 2500 feet in elevation and seems second in total area only to the two *Abies amabilis* zones within Mt. Rainier National Park.

The location of the six stands (3-8) of the *Tsuga heterophylla-Thuja plicata* community were as follows: stand 3, off State Route 5, 0.65 mile south of the Ohanapecosh Ranger Station; stand 4, near the Ohanapecosh Hot Springs campground, west of the Ohanapecosh River, 1/2 mile southwest of foot bridge; stand 6, same, but 1/2 mile northwest of foot bridge; stand 5, off Backbone Ridge road,

2.2 miles south from bridge over Ohanapecosh River; stand 8, same; stand 7, off State Route 5, 0.9 mile north of Ohanapecosh Ranger Station.

In the several stands of *Tsuga heterophylla-Thuja plicata* community, Douglas-fir commonly and western white pine (*Pinus monticola*) less frequently were observed as seral since they were not reproducing. As shown in table 3 these stands were predominantly of western hemlock although western red cedar could be found in lower moister spots in temporary stream channels, and on level flood plains. The area studied is characterized by relatively steep slopes and these were found to have a high proportion of western hemlock of all sizes, in some cases exceeding 4 feet DBH; young trees of western red cedar were appreciably fewer in number. Since a small hemlock 3 inches in diameter was observed to have more than 80 growth rings, a tree 2 feet in diameter could range up to several hundred years in age. In any case, these forests were judged to be quite mature and of considerable age; therefore the several stands were believed to constitute a good test of relationship of moss species to tree communities.

The undercover of these forests resembled that of Douglas-fir stands in having *Acer circinatum* and *Berberis nervosa*. However, *Gaultheria shallon* was absent or greatly reduced in coverage; and several other species appear to be common here which were not of importance under the Douglas-fir, e. g., *Vaccinium parvifolium*, *Cornus canadensis*, *Linnaea borealis* var. *americana* and *Tiarella unifoliata* (table 3). In addition some relationships appear here to the *Thuja plicata-Tsuga heterophylla* associations of the Rocky Mountains as described by Daubenmire (5).

The mosses in this community consisted primarily of *Rhytidopsis robusta*, *Euryhynchium oreganum*, and *Dicranum fuscescens*. *Rhytidopsis robusta* occurred largely on the ground layer—in particular on the well-littered soil characteristic of these forests—although it was found capable of growing over logs and rocks. *Dicranum fuscescens*, while common on the ground, was more frequently found on logs and tree bases. In addition to these species, *Hypnum circinale* occurred with a smaller percentage of coverage but with a high frequency; it was almost strictly confined to logs and tree bases although occasionally extending to compact litter.

A remarkable correlation appeared in coverage and frequency of *Rhytidopsis robusta* with *Tsuga* in both the *Tsuga heterophylla*-*Thuja plicata* and *Abies amabilis*-*Tsuga heterophylla* communities (table 3). The reason for this is not known, but it may be surmised that in this region the litter of western hemlock provides an especially suitable substrate for *Rhytidopsis robusta*. This seems the more plausible since a similar correlation was found with the essentially epiphytic or epixylic *Hypnum circinale*.

In contrast with the Douglas-fir community, *Hylocomium splendens* and *Rhytidadelphus triquetrus*—though common—were found to be of little quantitative significance, relatively, in the *Tsuga heterophylla*-*Thuja plicata* forests. Although many other bryophyte species may be found in this zone, relatively few are of significance quantitatively within the mature stands. Most of the many species collected in the area in the several visits of the authors appeared to occur as successional types on exposed mineral soil along road cuts, on rocks, in or by streams, etc. The current report has been restricted to the relatively few in study sites within a mature area of the forest.

Abies amabilis-*Tsuga heterophylla* community

At an elevation of approximately 2700 feet, and extending upward to about 3800 feet, the forest was found to be dominated by *Abies amabilis* with *Tsuga heterophylla* and *Thuja plicata* as lesser codominants. *Abies amabilis* extended beyond this range but constituted at the higher levels a distinctly different community with other tree species. In the *Abies amabilis*-*Tsuga heterophylla* community *Abies amabilis* showed a marked vigor of reproduction exceeding that of *Tsuga heterophylla* which in turn was above that of *Thuja plicata*. The sites where plots were studied were as follows: stand 9, off State Route 5 south of Deer Creek, 0.95 mile from Deer Creek bridge; stand 10, off State Route 5, just north of Deer Creek.

At this elevation the upper limit is approached for both Douglas-fir and western white pine but both were to be found in or near the stands as seral species. Also occurring within this range were some trees of *Tsuga mertensiana*, the mountain hemlock, and *Chamaecyparis nootkatensis*; however, these species do not appear to be constituents of the *Abies amabilis*-*Tsuga heterophylla* forests and were not found within the stands considered here.

Judging from the diameter of trees, these stands were as old or older than several of those below, since trees were found having a DBH as follows: Douglas-fir, 5+ feet; Pacific silver fir, 2+ feet; western hemlock, 3+ feet; western red cedar, 4 feet.

As might be expected, the undercover of this community differed markedly from the previous types. *Acer circinatum*, *Berberis nervosa*, and *Linaea borealis* var. *americana* were absent or infrequent and other species appear, e.g., *Rubus lasiococcus*, *Vaccinium ovalifolium*, and *V. membranaceum*.

The predominant moss species in this community, as in the *Tsuga heterophylla*-*Thuja plicata* forest, was *Rhytidopsis robusta*, with *Dicranum fuscescens* being second in abundance. A number of species of common occurrence under *Tsuga heterophylla*-*Thuja plicata* stands were not found in the *Abies amabilis*-*Tsuga heterophylla* community; these include *Hylocomium splendens*, *Eurhynchium oreganum*, *Rhytidadelphus loreus* and *Pseudisotrichium stoloniferum* (table 3). The absence of these moss species appeared to mark rather clearly the limits of these two tree communities.

Abies amabilis-*Tsuga mertensiana* community

Above the *Abies amabilis*-*Tsuga heterophylla* forest the species *Tsuga mertensiana* and *Chamaecyparis nootkatensis* assume dominance, generally at elevations between 4000 to 5000 feet. In this region evidence of the snow pack was found particularly marked by crusting of the litter and appearance of "snow mold." The stands here appeared to have a somewhat more open canopy than those of other communities below. Douglas-fir and western white pine were not observed here. There is some occurrence in the same elevation range of *Abies lasiocarpa* and of *Abies nobilis*.

The sites on which plots were located were as follows: stand 11, off State Route 5, 0.2 mile from bridge, south of Dewey Creek; stand 12, 0.55 mile north of Cayuse Pass road junction, off of U. S. Route 410.

The shrub and herb vegetation of this stand were found to be quite distinctive (table 3) with *Menziesia ferruginea* and *Xerophyllum tenax* (on well-drained soil) making an appearance.

The mosses likewise are distinctive although greatly less in cover than in lower forests. *Rhytidopsis robusta* did not occur in any abundance in the absence of *Tsuga heterophylla*, although it was found in or near the stands. On the other hand *Dicranum fuscescens* occurred in abundance about equal to that in the *Abies amabilis-Tsuga heterophylla* forests. Although extensive data were not obtained in this community, a marked difference in the moss communities seems apparent.

Abies lasiocarpa community

Above the *Abies amabilis-Tsuga mertensiana* community the forest gradually gives way to isolated clusters of trees surrounded by subalpine meadows; the latter merge above with the alpine zone. The dominant tree in the subalpine range is *Abies lasiocarpa*, which, in the Mt. Rainier region, was observed to be associated in some places with *Tsuga mertensiana* and *Pinus albicaulis*.

Only one site was studied. This stand, no. 13, was located 1.6 miles southwest of the view point on Sunrise Ridge below Yakima Park.

The data—which conform to observations on several visits—indicate that in this community also there were distinctive features of the moss layer. Unlike the communities below, in which there was a denser forest cover with a conspicuous duff layer over which mosses grew, the subalpine mosses appeared largely to be forms characteristic of mineral soils. *Polygonatum alpinum*, *Polytrichum piliferum*, and *Bryum pallescens* are species characteristic of a mineral soil substrate. This observation conforms with the evidence of the high degree of rodent activity in disturbing the soil surface and the absence of a thick duff in most of the plots. Within the clumps of trees a distinct litter was found but the mosses which appeared here seemed to grow on the mineral soil and to push up through the litter rather than grow on it.

DISCUSSION

The results of the present study clearly show several features of interest with respect to both frequency and coverage of bryophytes in climax forest stands. There is a predominance of a few (2 or 3) moss species in each community. Each tree community is associated

with a characteristic bryophyte community. In general the moss species of significant frequency or coverage values are not restricted in range to a given community but rather appear to be restricted primarily in relative abundance. This is interpreted as indicating that the correlation of moss species with tree species is due to a coincidence of favorable ecologic factors and species requirements. More specifically it may be inferred that in this particular area certain bryophyte species are favored by the presence of particular tree species. Some possible factors are suggested by the influence of leaf litter of various tree species in the Pacific Northwest on soil pH and nutrient materials (5, 6).

In the present study three species of mosses seem well correlated with certain tree species. These are: *Eurhynchium oreganum* with *Pseudotsuga menziesii*; *Rhytidopsis robusta* with *Tsuga heterophylla*; and *Hypnum circinale* with *Tsuga heterophylla*. The high coincidence of these species seems too great for chance. The present study serves simply to show that the relationship seems quite constant but does not reveal the cause of it.

Although some of the predominant moss species are quite restricted, others appear to be widespread and, perhaps, characteristic of coniferous forests across the continent or around the northern hemisphere. *Hylocomium splendens* and *Rhytidadelphus* species are of ecologic importance in North America and in Europe (7). The following species appear to be of importance in both the Pacific Northwest (present study) and, under different dominant trees, in the Appalachians (4, 9): *Hylocomium splendens*, *Rhytidadelphus triquetrus*, *Dicranum fuscescens*, and *Plagiothecium denticulatum*. Thus the moss communities of forest associations may have both widely ranging elements and quite restricted forms. Such combinations—together with the responsiveness of the bryophytes to various environmental factors—give considerable promise that an increasing knowledge of moss societies may be very useful in characterizing more precisely the community as a whole.

SUMMARY

1. Frequency and coverage estimates of terrestrial mosses and higher plants were made in thirteen forest stands, at different elevations, tentatively classified into five climax communities.

2. A test of the method, in which 25 one-tenth meter plots usually were estimated, revealed that (in one locality) as few as 10 plots gave number-of-species and species-coverage estimates close to those of 50 plots.

3. Each tree community appears to have a characteristic bryophyte layer with two or three moss species predominant.

4. In the *Pseudotsuga menziesii* community, lowermost altitudinally, *Eurhynchium oreganum*, *Hylocomium splendens*, and *Rhytidadelphus triquetrus* were found to be predominant species of the moss layer. *Eurhynchium oreganum* was found also in the *Tsuga heterophylla*-*Thuja plicata* community in amounts related to the abundance of *Pseudotsuga menziesii* and *Acer circinatum*.

5. The predominant moss in five stands of the *Tsuga heterophylla*-*Thuja plicata* community was *Rhytidopsis robusta* with *Eurhynchium oreganum* and *Dicranum fuscescens* occurring as less important quantitatively. Other less abundant mosses, such as *Rhytidadelphus loreus* and *Pseudisothecium stoloniferum*, were usually present in these stands.

6. In the *Abies amabilis*-*Tsuga heterophylla* community, at altitudes above the *Tsuga heterophylla*-*Thuja plicata* community, *Rhytidopsis robusta* was the predominant moss. This species thus seems correlated with the occurrence of *Tsuga heterophylla*. Also, in this stand, *Dicranum fuscescens* had relatively high frequency and coverage values; *Rhytidadelphus loreus* and *Pseudisothecium stoloniferum* were absent.

7. At higher elevations, in the *Abies amabilis*-*Tsuga mertensiana* community, *Dicranum fuscescens* was predominant but the percentage area covered by mosses was less than that in lower forests. *Rhytidopsis robusta*, though present, was insignificant in frequency or coverage.

8. It is suggested that the correlation of a moss species with a tree species, e.g., *Rhytidopsis robusta* with *Tsuga heterophylla*, may be due to an effect of the tree litter on the soil pH or nutrients creating conditions favorable to the moss species.

ACKNOWLEDGMENT

The authors are pleased to acknowledge the aid of Dr. R. Daubenmire for his constructive criticism of the manuscript and of Dr. H. S.

Conard for kindly checking the identification of most of the moss species.

LITERATURE CITED

1. BRAUN-BLANQUET, J. (translated and edited by G. D. Fuller and H. S. Conard). *Plant Sociology*. Pp. XVIII-439. McGraw-Hill Book Co., New York. 1932.
2. BROCKMAN, C. F. *Flora of Mt. Rainier National Park*. U. S. Government Printing Office, Washington, D. C. 1947.
3. CAIN, S. A. AND W. T. PENFOUND. *Aceretum rubri*; the red maple swamp forest of central Long Island. *Amer. Midl. Nat.* 19:390-416. 1938.
4. CAIN, S. A. AND A. J. SHARP. Bryophytic unions of certain forest types of the Great Smoky Mountains. *Amer. Midl. Nat.* 20:249-301. 1938.
5. DAUBENMIRE, R. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. *Ecol. Monog.* 22:301-330. 1952.
6. DAUBENMIRE, R. Nutrient content of leaf litter of trees in the northern Rocky Mountains. *Ecology* 34: 786-793. 1953.
7. GAMS, H. *Bryo-cenology (moss-societies)*. Chapter 12:323-366, in *Manual of Bryology*. Fr. Verdoorn, editor. The Hague. 1932.
8. ILVESSALO, Y. Notes on some forest (site) types in North America. *Acta forest. fenn.* 34(39):1-111. 1929.
9. OOSTING, H. J. AND W. D. BILLINGS. A comparison of the virgin spruce-fir forest in the northern and southern Appalachian system. *Ecol.* 32:84-103. 1951.

TABLE 3

The frequency and coverage of bryophytes in relation to other vegetation in thirteen stands of coniferous forests. The figures are from 25 1/10 meter plots except as otherwise noted.¹ Both frequency and coverage are reported as percentages, frequency being the figure to the left in each column. "C" indicates a species considered to be climax, "S" a species considered serial for the stand, "X" indicates occurrence in or near the stand. (Species occurring in only one plot, or within one stand, and not in a plot, are listed below the table.)

Stand No.	1	2	Climax dominants				Abies amabilis-Tsuga heterophylla				Abies amabilis-Tsuga mertensiana				Abies lasiocarpa	
			3	4	5	6	7	8	9	10	11	12	13			
TREE SPECIES																
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	C/87	C/73	s/60	s/32	s/1	s/17	X		s/12	X		X				
<i>Tsuga heterophylla</i> (Raf.) Sarg.	C/80	C/39	C/87	C/52	C/87	C/75	C/15	C/-								
<i>Thuja plicata</i> Lamb.	C/49	X	C/14	X	C/5											
<i>Pinus monticola</i> Dougl.			s/12	X												
<i>Abies amabilis</i> (Loud.) Forbes							C/77	C/-	C/44	C/-						
<i>Tsuga mertensiana</i> (Boug.) Sarg.									C/33	C/-						
<i>Chamaecyparis nootkatensis</i> (Lamb.) Spach.																
<i>Abies lasiocarpa</i> (Hook.) Nutt.															C/46	

¹ The number of plots for stand No. 5 was 10, for No. 10 was 50, for No. 11 was 8, and for No. 13 was 12.

TABLE 3—(Continued)

Climax dominants	Pseudotsuga menziesii	Tsuga heterophylla-Thuia plicata						Abies amabilis-Tsuga heterophylla	Abies amabilis-Tsuga mertensiana	Abies lasiocarpa			
		1	2	3	4	5	6	7	8	9	10	11	12
BRYOPHYTE SPECIES													
<i>Eurhynchium organum</i> (Sulliv.) Jaeger and Sauerb.	92/8	92/33	80/8	56/7	50/0	40/8	4/0						
<i>Hylocomium splendens</i> (Hedw.) Bry. Eur.	84/21	12/2	24/7	X	10/0	8/0	X						
<i>Rhytidadelphus triquetrus</i> (L., Hedw.) Warnst.	84/9	48/12				8/0							
<i>Camptothecium megaphilum</i> Sull.	12/0	X	4/0		10/0								
<i>Rhytidopsis robusta</i> (Hook.) Broth.	12/1	100/52	72/10	90/33	84/28	96/57	96/28	92/33	92/39	X			
<i>Dicranum fuscescens</i> Turn.	4/0	20/1	36/1	8/0	20/0	44/4	36/4	28/3	56/6	68/12	38/5		
<i>Neckera douglasii</i> Hook.	X	X	X	X	X								
<i>Antitrichia curtipendula</i> (Hedw.) Brid.	X	X						X					
<i>Rhytidadelphus loreus</i> (L., Hedw.) Warnst.	X		12/3	8/1	X	4/0	X		X				
<i>Dicranum strictum</i> Schleich.	8/0												
<i>D. scoparium</i> (L.) Hedw.	8/0	4/0											
<i>Hypnum circinale</i> Hook.	16/0	12/0	20/0	40/5	40/5	32/3	16/0						
<i>Plagiothecium denticulatum</i> (L., Hedw.) Bry. Eur.	4/0	24/1		X	4/0	8/0	32/1	6/0	16/0				

TABLE 3—(Continued)

Stand No.	Climax dominants	Pseudotsuga menziesii	Tsuga heterophylla/Thuja plicata					Abies amabilis-Tsuga heterophylla			Abies amabilis-Tsuga mertensiana			Abies lasiocarpa	
			1	2	3	4	5	6	7	8	9	10	11	12	
	<i>Pseudisothecium stoloniferum</i> (Hook.) Grout		4/0	8/0	X	X	X								
	<i>Heterocladium procurrens</i> (Mitt.) Rau and Hervey		4/0		X			10/0							
	<i>Ptilidium californicum</i> (Austin) Underwood and Cook														
	<i>Pseudoleskeia atrovirens</i> Dicks., Bry. Eur.														
	<i>Porella navicularis</i> (Lehm. and Lindenb.) Lindb.														
	<i>Pseudoleskeia oligocladia</i> Kindb.														
	<i>Cladopodium bolanderi</i> Best														
	<i>Burbaumia piperi</i> Best														
	<i>Mnium spinulosum</i> Br. and Sch. Bry. Eur.														
	<i>Brachythecium plumosum</i> (sw.) Br. and Sch. var. <i>roellii</i> (R. and C.) Grout?														
	<i>Scapania bolanderi</i> Austin														

TABLE 3—(Continued)

Climax dominants	<i>Pseudotsuga menziesii</i>	<i>Tsuga heterophylla-Thuja plicata</i>				<i>Abies amabilis-Tsuga heterophylla</i>		<i>Abies amabilis-Tsuga mertensiana</i>	<i>Abies amabilis-Tsuga mertensiana</i>				
Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Blepharostoma trichophyllum</i> (Linné) Dumortier		X		X	X								12/0
<i>Lophocolea heterophylla</i> Schrader				X					X				X
<i>Cephalozia pleniceps</i> (Austin) Lindb.					X				X				X
<i>Arctoa starkei</i> (Web. and Mohr.) Grout						X				X			X
<i>Brachythecium leibergii</i> Grout							X						
<i>Pogonatum alpinum</i> (Hedw.) Roehl.								X					
<i>Bryum palescens</i> Schleich.													
SHRUB AND HERB SPECIES													
<i>Acer circinatum</i> Pursh.	C/10	C/7	C/16	C/22	C/1	C/2	C/5						
<i>Achlys triphylla</i> (Smith)	76/15			32/8	10/0	24/2	32/6	X					
D.C.	56/15	96/47	4/0		20/0	8/0		X					
<i>Gaultheria shallon</i> Pursh.	52/4	68/11	28/5	40/6	40/2	16/0	36/9	4/0					
<i>Berberis nervosa</i> Pursh.	16/0	12/1											12/1
<i>Symphorocarpos mollis</i> Nutt.													8/0

TABLE 3—(Continued)

Climax dominants	Pseudotuiga menziesii		Tsuga heterophylla-Thuja plicata				Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa			
	Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Rubus macropetalus</i> Dougl.	X			8/0										
<i>Trientalis latifolia</i> Hook.	24/2	12/0												
<i>Goodyera oblongifolia</i> Raf.	8/0													
<i>Cornus canadensis</i> L.	8/0		16/1	8/2										
<i>Chimaphila umbellata</i> (L.) Bart. var. <i>occidentalis</i>														
(Ryd.) Blake	16/0													
<i>Arenaria macrophylla</i> Hook.	16/0													
<i>Lactuca biennis</i> (Moench.) Fern.	16/0													
<i>Collomia heterophylla</i> Hook.														
<i>Pteridium aquilinum</i> (L.) Kuhn var. <i>lamegosum</i>	12/0													
(Bong.) Fernald	8/2	4/0	4/0											
<i>Vaccinium parvifolium</i> Smith	4/0	32/3	24/8	20/0	12/0	16/0								
<i>Limnaea borealis</i> L. var.														
<i>americana</i> (Forbes) Rehder	4/0	X	32/8	30/2	32/1	40/10	20/2							
<i>Tiarella unifoliata</i> Mitt.	12/1	44/10	10/0											
<i>Viola sempervirens</i> Greene	8/1		30/0											
<i>Chimaphila menziesii</i> (R. Br.) Spreng.														
<i>Pachistima myrsinites</i>		4/1												
										X				

TABLE 3—(Continued)

Climax dominants	Stand No.	1	2	Tsuga heterophylla-Thuja plicata				Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa
				3	4	5	7	8	9	10	11	
(Pursh.) Ref.		4/0		10/0								
<i>Monotropa hypopitys</i> L.		X										
<i>Trillium ovatum</i> Pursh.		X		4/0								
<i>Corallorrhiza mertensiana</i>												
Bong.		X										
<i>Listera caurina</i> Piper		X										
<i>Mitella caulescens</i> Nutt.		4/0		28/2								
<i>Clintonia uniflora</i>												
(Schnitzl.) Kunth.												
<i>Gaultheria ovalifolia</i> Gray												
<i>Vaccinium ovatum</i> Pursh.												
<i>Ophiorrhiza horridum</i>												
(Smith) Miguel												
<i>Rubus lasiococcus</i> A. Gray												
<i>Vaccinium</i> sp.												
<i>Rubus pedatus</i> Smith												
<i>Vaccinium ovalifolium</i> Smith												
<i>Vaccinium scoparium</i> Leiberg												
<i>Pyrola secunda</i> L.												
<i>Vaccinium membranaceum</i>												
Doug.												
<i>Menziesia ferruginea</i> Smith												

TABLE 3—(Continued)

Stand No.	Climax dominants		Pseudotsuga menziesii			Tsuga heterophylla-Thuja plicata			Abies amabilis-Tsuga heterophylla		Abies amabilis-Tsuga mertensiana		Abies lasiocarpa	
	1	2	3	4	5	6	7	8	9	10	11	12	13	
<i>Rubus spectabilis</i> Pursh.														12/0
<i>Athyrium filix-femina</i> (L.)														12/2
Roth.														
<i>Phegopteris dryopteris</i> (L.)														12/0
Fee														50/12
<i>Sirex tripus curvipes</i> Vail.														
<i>Xerophyllum tenax</i>														
(Pursh.) Nutt.														
<i>Rhododendron albiflorum</i>														
Hook.														
														-/16

The shrub and herb species in stand No. 13 were as follows: *Valeriana sitchensis* Bong.; *Erythronium grandiflorum* Pursh. var. *pallidum* St. John; *Polemonium columbianum* Rydb.; *Viola* sp. (yellow); *Anemone occidentalis* S. Wats.; *Veratrum escholtzii* Gray; *Luzula glabrata* (Hoppe) Desf.; *Veronica cusickii* Gray; *Phlox diffusa* Benth.; *Vaccinium deliciosum* Piper; *Castilleja* sp.; *Sorbus occidentalis* (Wats.) Greene.

TABLE 3—(Continued)

The following bryophyte species occurred in only one plot or, in one stand (with insignificant frequency and coverage): *Mnium venustum* Mitt. in No. 1; *Polytrichum juniperinum* Hedw. in No. 2; *Bryum sandbergii* Holz. in No. 2 (?) and No. 8; *Dicranoweisia cirrata* (L., Hedw.) Lindb. in No. 2; *Calliergonella schreberi* (Willd., Br. and Sch.) Grout in No. 2; *Drepanocladus uncinatus* (Hedw.) Warnst. in No. 4; *Mnium punctatum* (L.) Hedw. in No. 4; *Tetraphis geniculata* Grgens. in No. 4; *Mnium menziesii* (Hook.) C. Muell. in No. 6; *Lepidozia reptans* (L.) Dum. in No. 7; *Mnium blyttii* Br. and Sch. Bry. Eur. in No. 9; *Dicranoweisia crispula* (Hedw.) Lindb. in No. 10; *Racomitrium heterostichum* var. *sudeicum* (Funk) Jones in No. 11; *Andreaea rupestris* Hedw. in No. 12; *Racomitrium patens* (Hedw.) Huebn. in No. 12; *Polytrichum piliferum* Hedw. in No. 13; *Bryum caespiticium* (L.) Hedw. in No. 13; and *Pohlia* sp. in No. 13.

The following shrub and herb species occurred in only one plot or, in one stand (with insignificant frequency and coverage): *Rosa* sp. in No. 1; *Adenocaulon bicolor* Hook. in No. 2; *Campanula scouleri* Hook. in No. 2; *Dryopteris dilatata* (Hoffm.) A. Gray in No. 4; *Maianthemum dilatatum* (Wood) Neis. and Macbr. in No. 4; *Smilacina* sp. in No. 5; *Rubus nivalis* Dougl. in No. 6; *Viola adunca* J. E. Smith in No. 6; *Rosa gymnocarpa* Nutt. in No. 7; *Rubus* sp. in No. 7; *Allotropa virgata* T. and G. in No. 8; and *Streptopus amplexicaulis* (L.) D. C. in No. 11.

AN INTERESTING MEGASPORE SPECIES FOUND IN INDIANA BLOCK COAL¹

By G. K. GUENNEL²

Specimens of Block coal collected during the past 5 years for miospore analysis have aroused the curiosity of both geologists and the author. Many reddish-brown specks have been observed on bedding planes with the naked eye. Because of their abundance in the Block coals, megaspores were believed to provide an additional statistical aid in correlating coals. Finally, during the summer of 1954, a study of these large spores was undertaken. Unfortunately, the preliminary work, especially preparing coal samples for study and assembling widely scattered literature on megaspore analysis, proved more time-consuming than was anticipated. The author, however, expects to continue these studies and hopes that the later report will provide an additional means of correlating coals.

This report is concerned primarily with the great variation of spore morphology encountered in attempting to identify certain spores. The wide-field stereoscopic microscope used to scan the macerated coal for spores has insufficient magnification to enable differentiation of morphological characteristics. On the other hand, the dense, opaque spores proved to be difficult objects to examine under the biological scope. Arnold (1950, pp. 97-98) shows figures of spores photographed with transmitted light and red filters to bring out details of the more or less opaque spore body. This method was tried, and a red Wratten filter, F 29, proved to be satisfactory, especially for photographing specimens. (See figs. A and B, pl. 1.) The thinner, more translucent parts are best viewed and photographed with unfiltered light. For certain spores a combination of filters,

F 29 and D45, the latter a purple filter, gave the best results. The two-filter method proved unsatisfactory, however, when applied to photomicrography.

¹ Published with permission of the State Geologist, Indiana Geological Survey.

² Paleobotanist, Indiana Geological Survey.

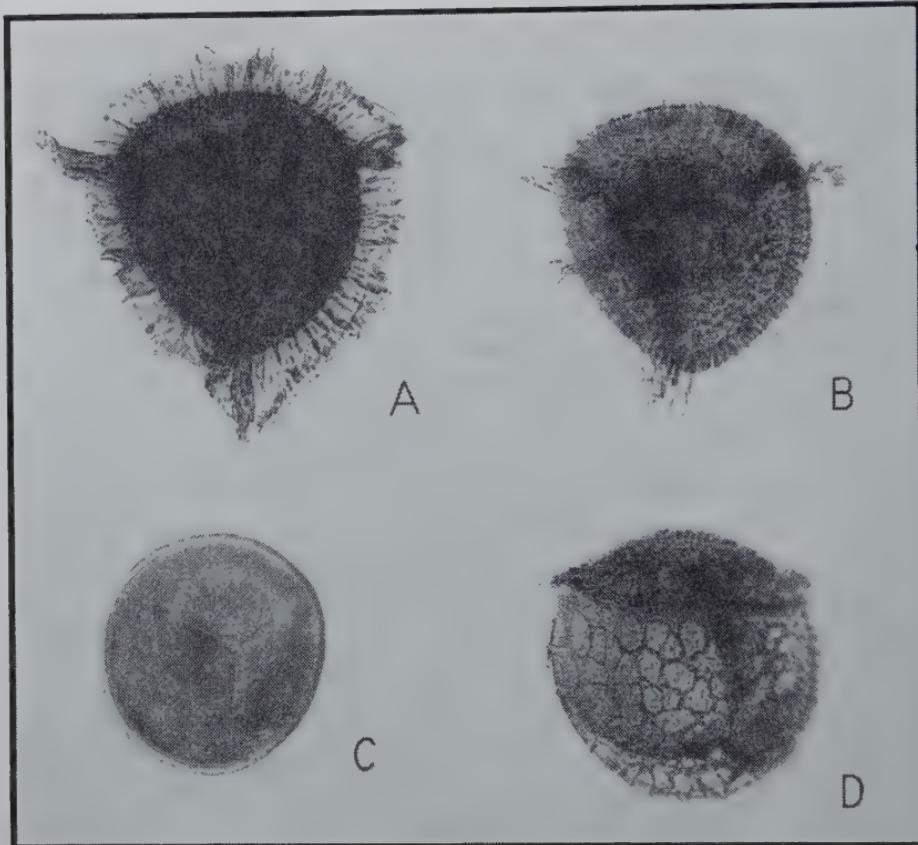


Plate 1

Photomicrographs of *Triletes triangulatus* Zerndt. $\times 50$

A. Specimen photographed without filter to show flange.

B. The same specimen photographed with Wratten filter F 29 to show details of body structure.

C. Spore without perisporal membranes, showing suture and mesospore.

D. Spore showing details of reticulum.

Filter F 29 was used to photograph specimens shown in C and D.

Many problems arose in attempting to identify the spores. In order to facilitate identification, a key was prepared, based mainly on the work of Schopf, Wilson, and Bentall (1944) and Dijkstra (1946). Many of the spores that were difficult to identify were finally classified as *Triletes gymnozonatus* Schopf, even though Dijkstra (1946) had made *T. gymnozonatus* synonymous with *T. triangulatus* Zerndt. Dijkstra's figure (1946, fig. 32, pl. 4), a photograph taken with reflected light, showed the trilete mark extending to the periphery of the spore. The spores whose identity was in

doubt had shorter trilete markings; many of the sutures were split open. A large number of spores had equatorial flanges and body reticulations. These spores could be assigned to *T. triangulatus* without great difficulty. Tracing the "unknown" spores individually through the key proved unprofitable. Viewing the assemblage as a whole, however, brought to light several differentiating features. Some of the round spores had well-defined trilete rays, but they differed from *T. gymnozonatus* by having body reticulations. Others did not have reticulations and the trilete scar was obliterated by membranous lamellae. Some smooth spores had flanges or pointed, ear-like projections. In most spores three of these "ears" were visible, but in some only one or two could be seen. After much effort to classify these odd spores had been spent, an experiment was undertaken. Some typical *T. triangulatus* specimens were glued to cardboard slides. With the aid of a finely drawn-out glass tube and a single bristle attached to a glass rod, the flange was torn off the spore body. This operation, performed under the stereoscopic microscope, yielded rather startling results. In several specimens the flange and lamellae were seen to be connected, as the triradiate lamellae remained attached to the flange when the latter was pulled off. A thin reticulate membrane was attached to some flanges. Other denuded spores retained fragments of the reticulum and some spores retained even parts of the flange. It soon was evident that the flange, lamellae, and reticulum constituted a single membranous complex. This complex was found to be attached at the base of the flange and along the triradiate scar. The flange is attached to the spore body slightly above the equator, that is, toward the proximal surface of the spore. Although the author failed to demonstrate satisfactorily that the lamellae are attached as described below, several specimens seemed to have either bifurcate lamellae or two lamellar membranes lining each scar. The author believes that the latter is correct, but thinks that there are three lamellae. Each one is connected to the flange at two places and lines two rays. Figure 1 illustrates the lamellar structure as visualized by the author. The diagram shows the lamellae flattened out. As two lamellar membranes line each ray and lamellar folding tends to be prevalent, one can readily understand why the triradiate markings can be hidden.

The "ears" found protruding in many spores are simply extensions of the triradiate lamellae overlapping the pointed, widened areas

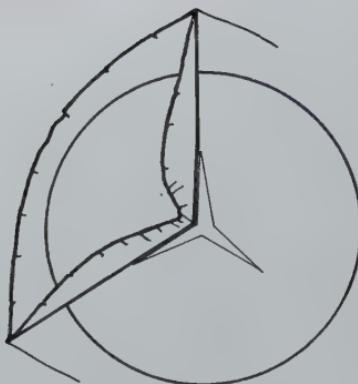


Fig. 1. Diagram showing flange and lamella relationship.

of the flange. Since there are at least two layers of membrane in these areas (possibly three if the two-lamellae theory is correct), less folding takes place in the areas opposite the ray termini. These more rigid and thicker areas therefore tend to stick out, whereas the rest of the flange may be folded over or even torn away. Compression of spores along planes other than the equator, also may result in partial obliteration of the flange.

Dijkstra (1946, p. 53) said that spores of *T. triangulatus* are marked by perispores with reticulate structures but that the reticulum is not well developed on the proximal surface where the meshes are only from 17 to 25 microns wide. The well-defined reticulations on the distal side measure from 20 to 80 μ (see fig. D, pl. 1). Although the author has not been able to determine with certainty whether the perisporal reticulations extend to the proximal surface, he believes that the contact areas are free of perisporal membranes except for the lamellae lining the rays. Coarse granulations, resembling small papillae in places, can be observed on some specimens under reflected light. This ornamentation, however, may be the result of shrinkage or other physical alteration rather than meshes of a perisporal net. Arnold (1950, p. 75) noted a "dense growth of minute bristle-like papillae" on the contact surfaces of some specimens.

A small subtriangular area is visible around the proximal pole on a large number of "naked" spores. The area is bounded by slightly curved lines running from ray to ray and is believed to be the mesospore, since some torn specimens reveal another spore coat within the outer covering. Wicher (1934, p. 176) mentioned the triangular

mesospore, and Schopf (1938, p. 37) in some specimens noted a central body which he interpreted as a "shrunken endosporal membrane."

Zerndt (1930, pp. 51-54, figs. 19-30, pl. 7) differentiated two varieties of *T. triangulatus* and designated them with Roman numerals I and II. Stach and Zerndt (1931, p. 1123) added a third subtype or variety strictly on the basis of slightly smaller size. Ibrahim (1933, pp. 29-31, figs. 23-24, pl. 3) gave the varietal trinomial designations *T. triangulatus regalis* and *T. triangulatus secundus* to Zerndt's subtypes I and II respectively. Zerndt failed, however, to refer to varieties in his later works, and Dijkstra (1946, p. 53) implied that there is little validity in subdividing the species.

That *T. gymnozonatus* is actually the spore body of *T. triangulatus* seems to be well-established fact. The triangular outline of *T. triangulatus* is the result of the triradiate lamellae continuing into the flange, which is widened and pointed opposite the ray termini. There is little doubt that the spore proper, previously named *T. gymnozonatus* by Schopf, is ornamented with a perisporal network attached to the flange and the triradiate lamellae. Figure 2 shows two views of *T. triangulatus*.

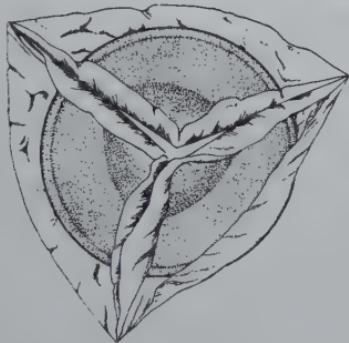


Fig. 2a. Drawing of *T. triangulatus* (proximal view).

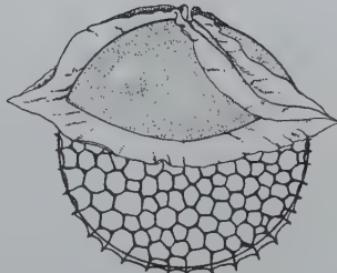


Fig. 2b. Drawing of *T. triangulatus* (side view).

The extensive synonymy given by Dijkstra (1946, pp. 52-53) need not be repeated here. Two species, which Dijkstra did not include, however, seem worthy of mention. In establishing the species *T. laxomarginalis*, Zerndt (1940, p. 136) stated that the spore is very similar to *T. triangulatus*, except for a larger spore body and a wider flange. The latter he never found intact. He found the species in only two samples from the Saar Basin and did not include it in his distribution charts because it was too rare. The species has not been

reported since. Unless two distinct size groups, based on definite measurements, were obvious to Zerndt,³ the retention of *T. laxomarginalis* as a species seems untenable.

Another species retained by Dijkstra, namely *T. artecollatus* Nowak and Zerndt, may be synonymous with *T. triangulatus*. This spore, according to Zerndt (1937, fig. 11), has open sutures and lacks a perisporal membrane but has the wall perforated with closely spaced, minute openings. Zerndt hinted that this perforated surface may be the result of maceration and that the outer surface of the spore coat is normally continuous and smooth. As far as can be determined, no one has reported the spore since. *T. artecollatus* may merely be the overmacerated spore body of *T. triangulatus*.

The retention of the two nomenclatorial entities, *T. triangulatus* and *T. gymnozonatus*, has no basis now that the relationship between the two "types" has been well established. Even a varietal designation, which would have some practical merit, since the frequently found naked spore body is quite distinct from the reticulate, flanged spore, seems no longer justifiable.

DESCRIPTION OF *TRILETES TRIANGULATUS* ZERNDT

The spore proper is round, smooth, and granular in texture (fig. C, pl. 1). The trilete scar in many spores is split open and extends about halfway to the spore periphery. Narrow lips line the sutures. Schopf (1938, p. 37) gave a size range of 500 to 600 microns; this coincides with the size measurements of the author. Zerndt (1934, p. 19), giving measurements exclusive of the flange for 12 specimens, stated that the specimens ranged from 238 to 531 microns in diameter, an average diametric measurement of 492 μ . The spore coat was from 20 to 30 μ thick.

A perisporal network is attached to the spore proper in many spores, but some spores lack this perispore. The perisporal membrane is reticulate on the distal surface. The meshes measure from 20 to 80 μ . This reticulate membrane may be fairly elastic and thus cause the reticulations to vary in size. If the membrane is loosely attached, the meshes seem larger, whereas a closely adhering mem-

³ This apparently was not the case, since he gave no measurements in the description of the species.

brane has smaller reticulations. The reticulum is attached to a flange which girdles the spore. Dijkstra (1946, p. 53) gave a range of 70 to 100 μ for the width of the flange and the author's measurements ranged from 55 to 120 microns. The flange broadens opposite the ray termini to form triangular, pointed, ear-like extensions, which give the spore a more or less triangular outline. Triradiate lamellae, which line the trilete rays, are attached to the flange at these areas. The lamellae are higher in the middle than they are at either end and may attain a height of 80 μ . The lamellae, as well as the flange, tend to be indented and undulating because of their fragility. They are highly translucent.

The proximal surface apparently is free of perisporal matter, except for the lamellae which line the rays, even though coarse granulations, resembling small papillae in places, cover the contact areas in some spores.

Size measurements, including equatorial flange, have been made by several authors. The minimum diametric measurement is 310 μ listed by Stach and Zerndt (1931, p. 1123). It is not clear, however, whether the flange was included in this measurement. The maximum size is 800 μ given by Dijkstra (1946, p. 53) and by Schopf (1938, p. 32). After measuring 100 specimens, the author found that the diameters range from 370 to 740 μ and that the average diametric measurement is 543.9 microns.

Schopf (1938, pp. 32-33) suggested that the megaspores classified under the form species *T. triangulatus* Zerndt are derived from herbaceous lycopods of the *Selaginellites* group.

T. triangulatus apparently has a wide geographical, as well as vertical, distribution. The species has been reported from the Calais and Nord Basins in France, from the Saar, the South Limburg Basin in Holland, from the Ruhr and Saxony Basins in Germany, from Upper Silesia and the Carpathian Basin in Poland, from Staffordshire, England, and from the Bohemian Basin in Czechoslovakia. In the United States the species has been found in Illinois, Michigan, Ohio, West Virginia, Kentucky, Pennsylvania, and now Indiana. Figure 3 shows the approximate vertical distribution of the species and relates European "Coal Measures" to North American stratigraphic units. Since little megaspore work has been done in the United

States, gaps in the distribution picture for America are due to the lack of information from those particular strata.

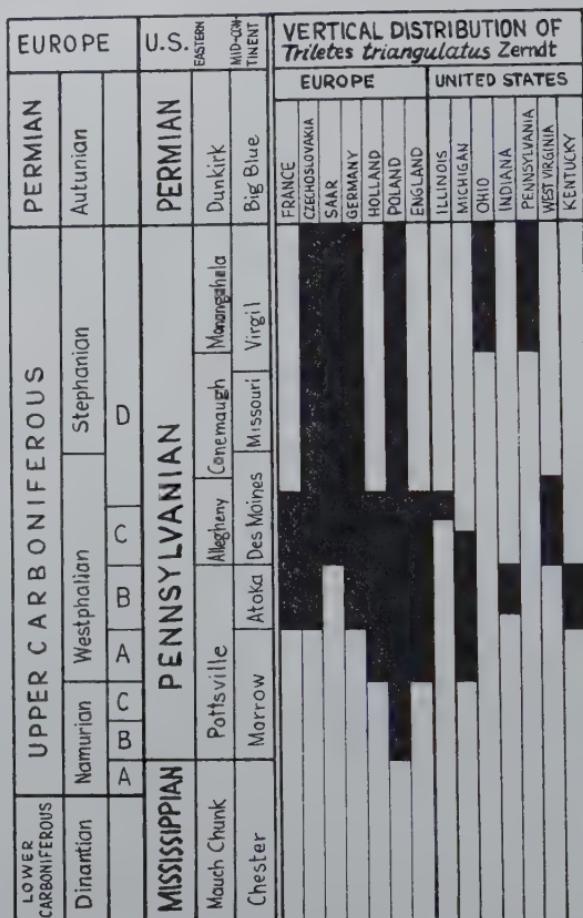


Fig. 3. Chart showing European and North American correlations and indicating the vertical distribution of *T. triangulatus*.

LITERATURE CITED

ARNOLD, CHESTER A. Megasporites from the Michigan Coal Basin. Contrib. Mus. Paleontol. Univ. Mich. 8(5): 59-111. 1950.

DIJKSTRA, S. J. Eine monographische Bearbeitung der karbonischen Megasporites. Mededel. Geol. Stich. C-III-1 (1): 5-101. 1946.

IBRAHIM, AHMEDJAN. Sporenformen des Aegirhorizonts des Ruhr-Reviers. Diss. Tech. Hochschule, Berlin. 48 pp. 1933.

SCHOPF, JAMES M. Spores from the Herrin (No. 6) coal bed in Illinois. Rept. Invest. Ill. Geol. Surv. No. 50. 55 pp. 1938.

_____, L. R. WILSON, AND R. BENTALL. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. Rept. Invest. Ill. Geol. Surv. No. 91. 77 pp. 1944.

STACH, E. AND J. ZERNDT. Die Sporen in den Flamm-, Gasflamm- und Gaskohlen des Ruhrkarbons. Glueckauf. 67 (35): 1118-1124. 1931.

WICHER, CARL A. Sporenformen der Flammkohle des Ruhrgebietes. Arbeit. Inst. Palaeobot. Petr. Brennst. 4 (4): 165-212. 1934.

ZERNDT, JAN. Megasporen aus einem Floez in Libiaz (Stephanien). Bull. internat. Acad. pol. sci. et lett. B: 39-70. 1930.

_____. Megasporen als Leitfossilien des produktiven Karbons. ibid. A: 165-183. 1931.

_____. Les megaspores du Bassin Houiller Polonais. I. Acad. pol. sci. et lett. Trav. geol. No. 1. 56 pp. 1934.

_____. Les megaspores du Bassin Houiller Polonais. II. ibid. No. 3. 78 pp. 1937.

_____. Megasporen des Saarkarbons. Palaeontographica. 84 (B): 133-150. 1940.

RE-EVALUATION OF THE DIATOM SPECIES *NITZSCHIA FRUSTULUM* (KUTZ.) GRUN.¹

By CHARLES W. REIMER²

INTRODUCTION

As in almost every other facet of science, the diatom taxonomist is constantly faced with the problem of merging phenomena. With the introduction of "quantitative," "mass," or "population" studies on various forms of plant life, lines of distinction between closely related species and varieties have often disappeared, thus indicating a single variable taxon (9). On the other hand, such studies have upheld the individuality of two or more similar taxa (1, 3). It is now amply apparent that many of the presently accepted species of diatoms must be re-examined with such concepts in mind, for the purpose of determining, in other than a purely arbitrary fashion, the limits of specific variation. This becomes especially important in this group. The most common method is asexual (7) in which case the size of the frustule frequently becomes gradually smaller, until a certain size range (10) is reached. Sometimes other taxonomic features are altered as well (4). If in a single ecological habitat intergrades are found between two entities, it usually is a good indication that a genetic difference does not actually exist, and that the investigator is dealing with a single entity.

Nitzschia frustulum belongs to the subgenus (or group) Lanceolatae and is taxonomically quite similar to several other species of *Nitzschia*. Occasionally these closely related forms are found in the same collection, in which case it is most difficult to categorize each specimen. With this in mind the present investigation was undertaken on some diatom populations collected in the United States and identified as having *N. frustulum* present.

¹ Presented before the American Society of Plant Taxonomists at the meeting in Gainesville, Florida, on September 6, 1954.

² Department of Limnology, Academy of Natural Sciences of Philadelphia, Philadelphia 3, Pennsylvania.

METHODS

Diatom material from three sources was used in this investigation: (1) Arizona, Mohave Co., river near Beaver Dam Lodge, Littlefield; (2) Texas, Calhoun Co., Mission Lake; (3) Pennsylvania, Chester Co., Ridley Creek near Chester Park. The first location can be considered as strictly fresh water, the second as brackish and the third as fresh to slightly brackish. These collections were selected for two reasons. They represent diverse habitats, and available slides from these locations had sufficient specimens for adequate measurement and comparison.

Specimens were observed under an oil immersion fluorite lens giving approximately 1,100 diameters magnification. Measurements on each specimen included length, width, striae number, keel punctae number, configuration of margins, and shape of ends. From each population, 110 specimens were observed. With each slide, specimens in the upper third of the cover slip were measured, continuous rows being observed until about one-third of the total 110 specimens had been tabulated. The slide was then shifted and the central and lower areas were scanned in turn, each area contributing another third of the total. Observations were selective only insofar as specimens of *Nitzschia* which obviously were out of the range of this particular group of the Lanceolatae were excluded. In counting keel punctae, the total number of punctae on one side was counted and from this data the average number in $10\ \mu$ was calculated. This differed from conventional methods of simply counting the keel punctae along a portion of the ocular micrometer. Since the spaces between keel punctae vary, it seemed that the former method represented a more constant and thus more reliable figure for comparison.

After these slides had been studied, an attempt was made to categorize the various forms observed. For comparison available slides of Van Heurck (authenticated by Grunow) were used, together with material from Rabenhorst's collection sent to the Academy through the courtesy of the Cryptogamic Herbarium of the American Museum of Natural History in New York City.

OBSERVATION AND RESULTS

The distribution of the "*Nitzschia frustulum*-like" specimens from Ridley Creek is shown in Fig. 1, where striae numbers are

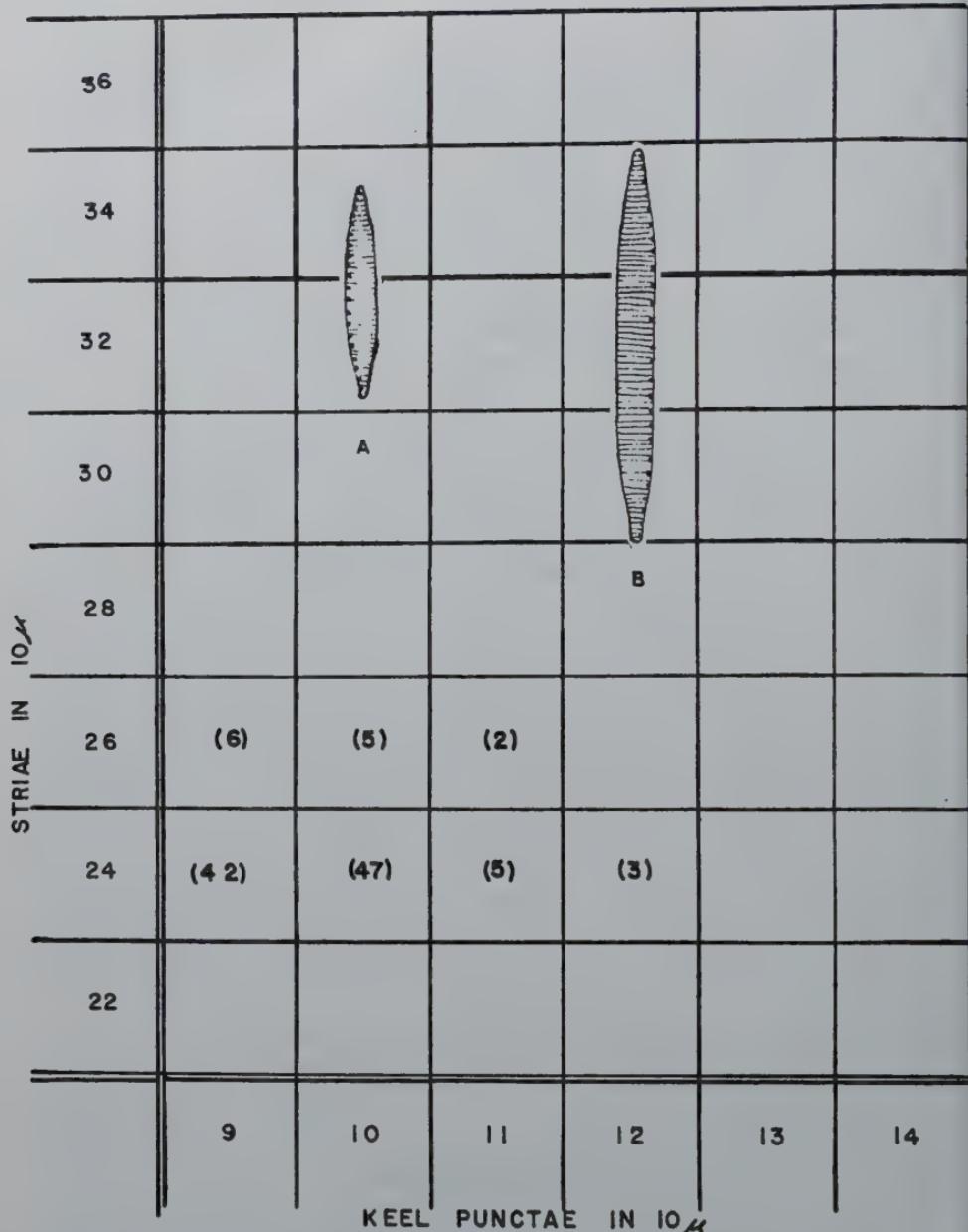


FIG. I. DIATOM POPULATION — RIDLEY CREEK, PA.

plotted against keel punctae numbers. The range of variation is seen to be quite restricted, the striae numbering between 24 and 26 in 10μ . Other measured data on the specimens plotted in Fig. 1 are shown in

Table 1. From this table it is seen that only 5 of the 110 specimens had both margins convex. The remaining ones varied from parallel to slightly concave. Some specimens had one parallel and one convex margin, a few had one parallel and one concave margin. The ends varied only slightly (Table 1). They were all obtuse, varying mostly in the amount of taper from the body to the tip. Also, depending on the position in which the diatom was situated, the ends appeared with a small knob-like extremity. The length varied from 13 to 42 μ ; the width held rather constant from about 3 to 4.5 μ .

TABLE 1
Populations of *Nitzschia frustulum*

Variation	Number of Specimens		
	Penna.	Ariz.	Texas
Length			
0-10	0	2	13
10-20	21	30	86
20-30	64	54	11
30-40	20	22	0
Over 40	1	2	0
Body Margins			
Both concave	24	4	0
Concave, straight	23	8	1
Both straight	47	64	9
Convex, straight	11	12	2
Both convex	5	22	98
Ends			
Fig. 1 A and B	110		
Fig. 2			
Type A		41	
Type B		10	
Type C and D		49	
Fig. 3			
Type A			37
Type B			41
Type C			20
Type D			12

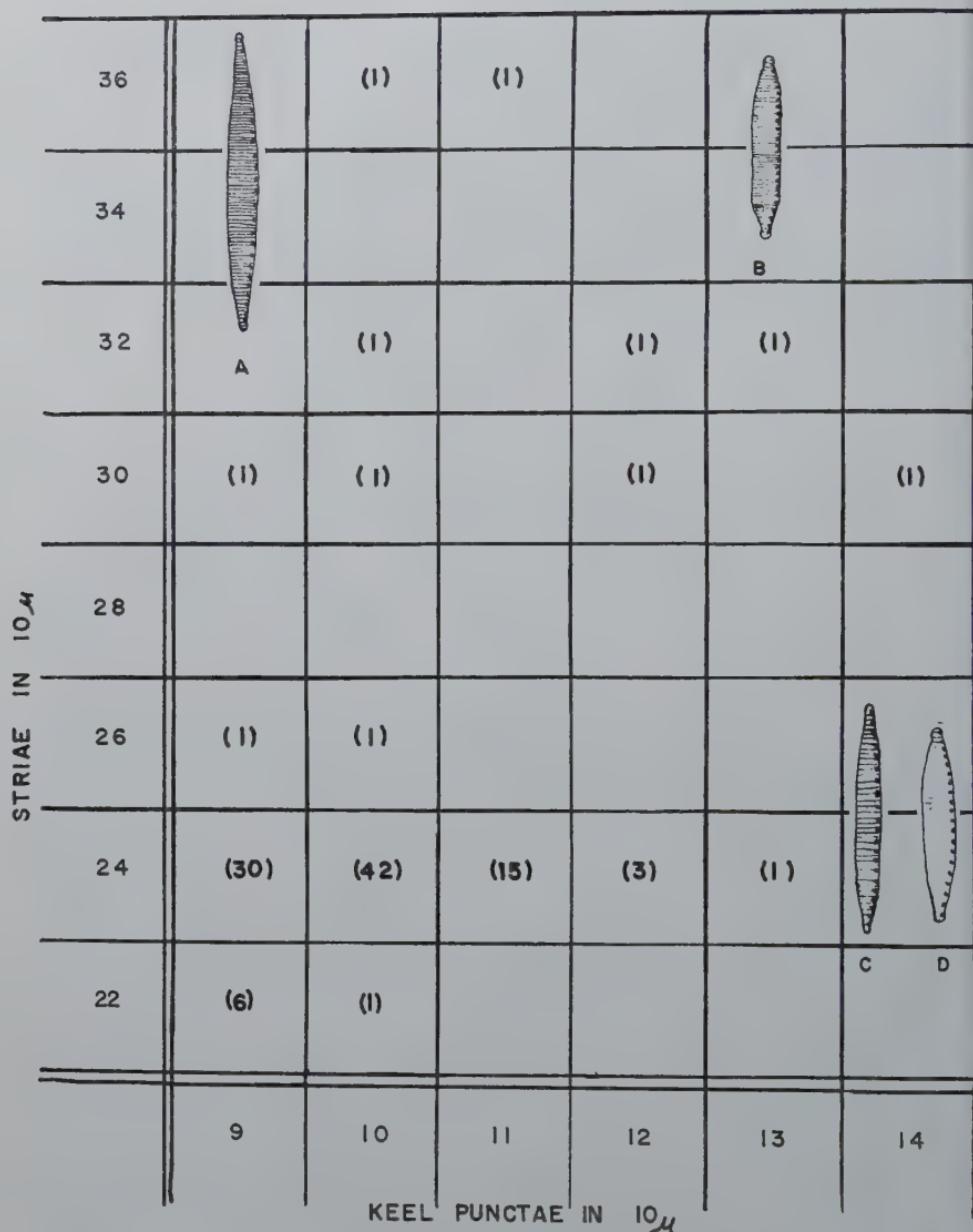


FIG. 2. DIATOM POPULATION—RIVER IN MOJAVE COUNTY, ARIZ.

The same plotting technique, as shown in Fig. 2, was applied to a diatom population from a river in Mojave Co., Arizona. Of the 110 specimens measured 72 were within a narrow range of 24 striae and 9 to 10 keel punctae in $10\ \mu$. Specimens immediately adjacent to this grouping brought the total up to 100. Only 10 specimens had striae 30 in $10\ \mu$ or above, thus setting them apart from the majority of specimens measured. These 10 specimens had a tendency to divide into two groups, those with keel punctae 9 to 11 and those with keel punctae 12 to 14 in $10\ \mu$. However, with the small number of specimens observed, it is difficult to determine if this difference be real or only apparent. Those specimens with a striae number of 30 or above had either parallel or convex margins; none had any indication of a concave margin. The larger grouping with striae from 22 to 26 varied as to body margin from concave to slightly convex. In most cases, a more definitely sub-capitate end was apparent in the group with finer striae.

In Fig. 3 are shown the ratios of striae to keel punctae as found in a population of diatoms from Mission Lake, Texas. Two groupings are apparent, the separation being mainly on the basis of striae number. Variation in number of keel punctae appears to be not too great. All specimens with finer striae (28 to 32 in $10\ \mu$) were quite small, varying in length from 5 to $13\ \mu$. In the grouping with coarser striae (22 to 24 in $10\ \mu$) variation in length was from 8 to $22\ \mu$. As in the specimens observed from Arizona, the more finely striae specimens from Mission Lake showed body margins varying from very slightly convex to strongly convex. In the coarsely striae specimens margins varied from one straight and one concave margin to those with both margins slightly convex. Neither group showed a characteristic type of end with the exception of specimens of Type C (Fig. 3) in which case the ends were slightly cuneate and sometimes had a small rounded knob-like end, not definitely capitate, however.

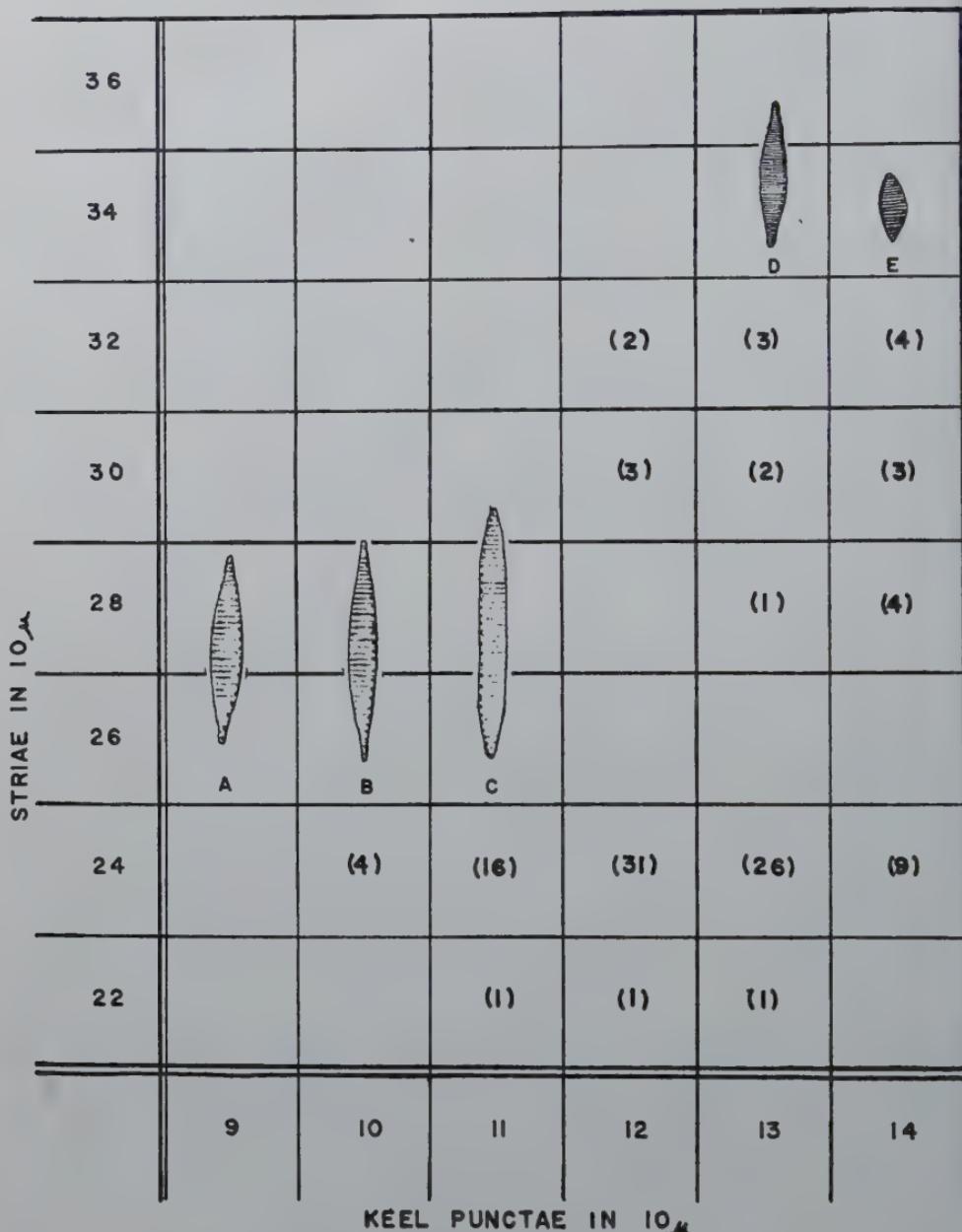


FIG. 3. DIATOM POPULATION—MISSION LAKE, TEXAS

Although the more coarsely striae specimens shown in Fig. 3 appear to form a single entity on the basis of striae to keel punctae ratio, there was a noticeable difference in body margins and ends

(Fig. 3, A. B. C. Table 1). All specimens of categories A and B, of which there were 63, had convex margins and attenuate narrow ends. Those of category C had concave, parallel or slightly convex margins.

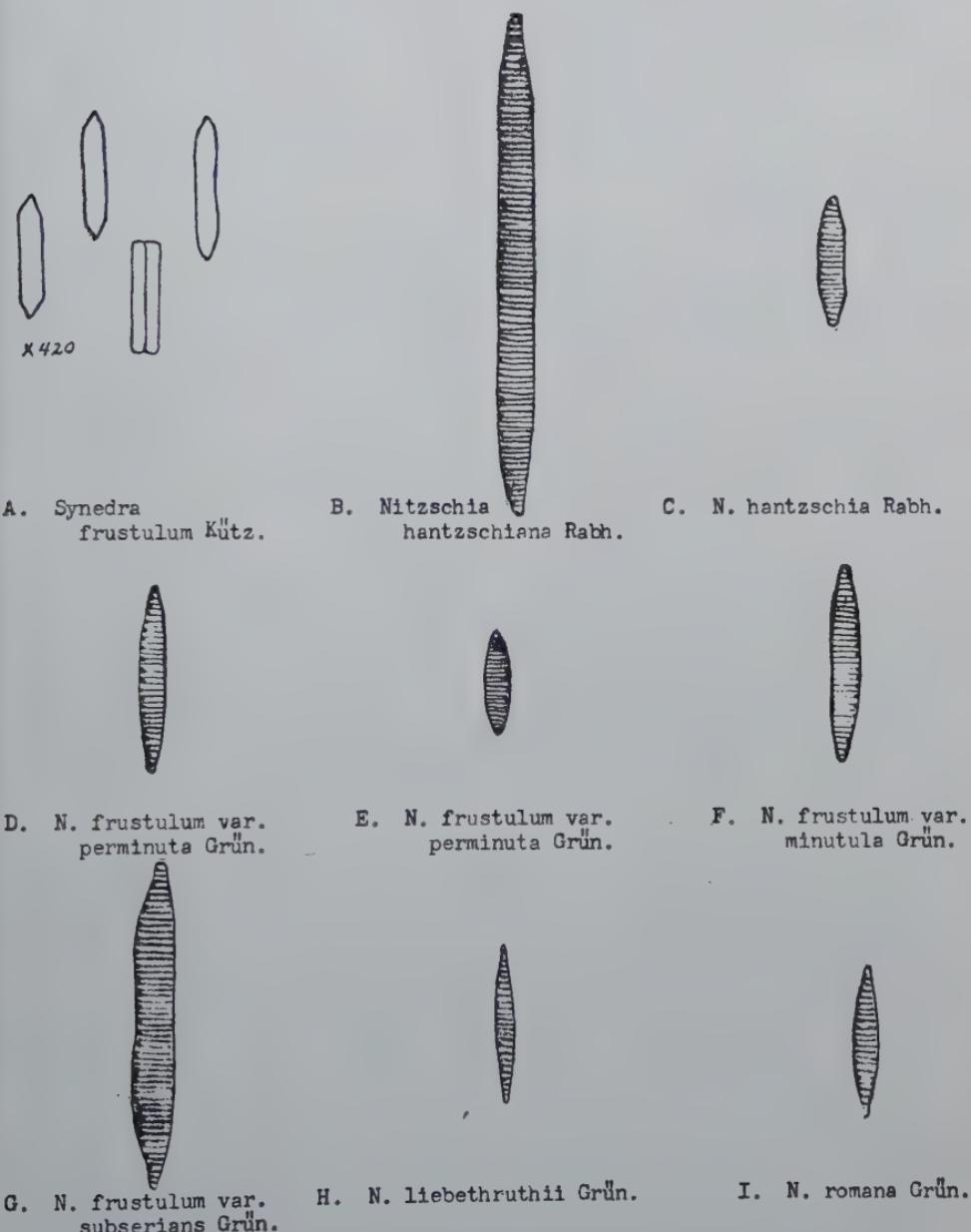


FIG. 4. FORMS PREVIOUSLY DESCRIBED

Ends were obtuse and somewhat cuneate, occasionally somewhat rounded off (Table 1). The smaller members of category C had convex margins somewhat as in category "E" but, of course, the striae number remained at 24 in 10 μ . Only those specimens below about 12 μ seemed to lose all indication of a nearly straight margin.

In an attempt to correlate the observed forms with described entities, material identified by Rabenhorst and slides authenticated by Grunow were examined. Fig. 4 shows the most common forms found on these slides.

DISCUSSION

The following range of variation has been given for *Nitzschia frustulum*:

	Kützing (6) (Fig. 4A)	Grunow (8)	Hustedt (5)
Length	20 μ	20-40 μ	20-70 μ
Width	?	4-5 μ	3-5 μ
Striae	?	20-22	20-23
Keel punctae	?	9-11	9-12
Ends	Cuneate-acute	Pointed	Cuneate-pointed

The species most closely associated with it are: *N. heufleuriana* Grun. and *N. hantzschiana* Rabh. The former is separated on the basis of its larger size (75-90 μ) and capitate ends; *N. hantzschiana* seems to overlap on all characters, but is said to differ by having coarser keel punctae (7-10 in 10 μ as opposed to 9-12 for *N. frustulum*) and mention is made of its being predominantly a montane form (5).

The majority of forms represented in Fig. 1 more closely resemble the description of *N. hantzschiana* than *N. frustulum*, in that the keel punctae number falls predominantly around 9 in 10 μ and the striae range is around 24 in 10 μ . With the method used in calculating keel punctae in 10 μ , the number would probably run one or two keel punctae higher than given in conventional descriptions. If two keel punctae per 10 μ were subtracted this would place the number within the range given for *N. hantzschiana*.

In the two remaining populations, types C and D in Fig. 2 and type C in Fig. 3 reveal a wider diversity in striae and keel punctae. Many specimens from Arizona (Fig. 2) duplicate those from Ridley Creek (Fig. 1) in general shape, ends, striae and keel punctae. The

majority of specimens of type C from Mission Lake, Texas, have a keel punctae number around 12 in $10\ \mu$, somewhat higher than in the other two populations, yet all other characters are identical and in these specimens (type C and D, Fig. 2, type C, Fig. 3) some would fit the description of *N. frustulum*, others would fit the descriptions for *N. hantzschiana*.

When the specimens of Rabenhorst were examined, it was apparent that the keel punctae number, by the conventional method along the ocular micrometer scale, varied from 9-12.5 in $10\ \mu$. The striae number remained constant at about 24 in $10\ \mu$ (Fig. 4B, 4C). This removes the major segregating factor between the two species, provided, of course, that the Kützing type slide shows the range of keel punctae given for *N. frustulum*.

It does not seem reasonable to separate the specimens on a striae difference of one or two striae, especially since this difference seems to disappear when several specimens are counted. Also the method of counting striae does not seem to the writer to be sufficiently accurate to permit distinction between 22, 23 or 24 striae in $10\ \mu$, especially when the specimens are small. In such a case a portion of the scale must be used and the striae count multiplied in order to get a count for $10\ \mu$. Only those counts varying more than two striae in $10\ \mu$ would appear practical for taxonomic differentiation in this group, especially in specimens with more than 20 striae in $10\ \mu$.

It is quite possible that certain selected habitats would favor the development of a clone such as *N. hantzschiana* over one like *N. frustulum*. This would account for separate identifications based on these small differences. On the basis of the specimens observed, it hardly seems justifiable to keep these two species as separate entities and it is proposed that they be drawn together under the earliest epithet, *N. frustulum*.

With the incorporation of these species it is also proposed that the lower limits of the size range be extended to forms as small as $10\ \mu$, the smallest forms of type C from Mission Lake. The upper limits may well reach to 70 (5), but in these populations only two specimens characteristic of *N. hantzschiana* exceeded $40\ \mu$, one being 41 and the other $51\ \mu$.

Forms A and B from Arizona (Fig. 2) probably represent the periphery of another population or populations. From their features it is possible that they represent forms of *N. palea* (Kütz.) W. Sm. although it is difficult to say without having analyzed other forms of *N. palea* which were present.

Forms D and E from Texas (Fig. 3) are very likely *N. fonticola* Grun., which has the shape of *N. romana* Grun. (Fig. 4I), but has finer striae (28-30 in 10 μ).

The remaining forms from Texas, A and B, differ from type C in having a characteristic narrow attenuate end, together with a consistently convex body margin. There appeared no clear-cut series of intermediate forms between these two. Until more such populations are observed it seems prudent to exclude this from the *N. frustulum* complex and consider it a form of *N. romana* (Fig. 4I) or *N. liebethruthii* Rabh. (Fig. 4H), two forms which do not differ significantly. These species are distinguished as follows:

	<i>N. liebethruthii</i>	<i>N. romana</i>
Length	11-27 μ	22-23 μ
Width	2-3 μ	4-5 μ
Striae	ca. 24 in 10 μ	23-24 in 10 μ
Keel punctae	ca. 12 in 10 μ	9½-11½ in 10 μ
Shape	pointed-lanceolate	lanceolate-linear lanceolate

Specimens observed showed no clear-cut tendency to fit either category. For example, most specimens measured between 3 and 4 μ in width and nearly all were less than 29 μ long. Keel punctae varied from 8 to 12 by usual methods of measurement. Evidence is not definite enough to categorize these specimens according to known taxa except to say that they appear closer to these two species than any other found described by the author. In the original description by Cleve and Grunow (2), it is suggested that *N. romana* may well be considered as a variety of *N. hantzschiana*. The solution to this problem must await further study and observation on specimens of *N. liebethruthii* and *N. romana*. Van Heurck (8) reports they have the same keel-punctae number and says further that the striae number varies by a single stria in 10 μ .

Diagrams of the specimens on the Van Heurck slide for *N. frustulum* var. *perminuta* Grun. (type locality) are given in Fig. 4D, 4E.

The striae on all specimens observed, ranged between 28 and 30 in 10 μ indicating that the variety is distinct enough from the species as described by Grunow to be retained as a variety of the species *N. frustulum*. Specimens labelled *N. frustulum* var. *minutula* Grun. (Fig. 4F) from the Van Heurck collection all have 24 striae in 10 μ . This does not agree with the original description of Grunow (8) which gives the striae number as 30 in 10 μ . Since the Van Heurck slide was authenticated by Grunow it represents the best specimens available for this variety. Since striae number is the only distinctive character, the variety should probably be included in the species. Several such forms were observed in the three populations studied.

N. frustulum var. *subserians* (Fig. 4G) agrees in all respects with the species description but appears most commonly with a conspicuously bilobate shape on the Van Heurck slide observed. Some specimens in the populations studied had a concave margin but did not show a clear indentation in the center. At present no conclusions as to the validity of this variety can be reached. If the bilobate feature appear constant a separate variety of *N. frustulum* may be retained. Otherwise it will probably be drawn into the species concept since all other features agree. It is hoped to present a second paper on this taxon including more of the named varieties and their possible position in the group. At present there is some question as to the validity of *N. inconspicua* Grun. and *N. perpusilla* both of which appear to be quite close to the *N. frustulum* taxon. In separating these various varieties earlier workers appear to have placed great emphasis on size and small variation in keel punctae number along with slight differences in striae number. Many of these differences disappear when populations such as these are observed.

SUMMARY AND CONCLUSIONS

1. Diatom collections from three locations in the U. S. A. were examined. Each collection was listed as having *N. frustulum* (Kütz.) Grun. present.
2. Populations of *N. frustulum*-like specimens were variously heterogeneous as shown in Figs. 1-3.
3. In each of the three localities studied there was present a continuous gradation of specimens ranging from those which could be

identified as *N. hantzschiana* Hantz. to those which could be identified as *N. frustulum*.

4. Since the two entities are very similar, the differences between them was further investigated. Specimens identified by Kützing as *Synedra frustulum* (original epithet for *N. frustulum*) were not available. The original description and plates of Kützing plus Grunow's and Hustedt's descriptions and plates were used as a basis of the concept of *N. frustulum*.

5. Species of *N. hantzschiana* Rabh. from the Rabenhorst collection No. 943 showed variation in number of keel punctae from 8 to about 12.5 in 10 μ . Striae number was always about 24 in 10 μ . Shape varied from slightly concave sides to somewhat convex margins in many of the smaller forms. These characters fall within the described range given for *N. frustulum*.

6. To say that *N. hantzschiana* prefers montane habitats in contrast to *N. frustulum* would not be in agreement with the findings in this investigation. Actually the species more nearly resembling the mid-range of *N. hantzschiana* were found in a stream on the Coastal Plain.

7. Since these two entities are so nearly the same in description and since good representatives of both were found in the collections studied in addition to intermediate forms, it is here proposed to unite the two under the earliest legitimate epithet, *N. frustulum* (Kütz.) Grun.

8. Other entities very closely related to this taxon were found. Their probable descriptions are discussed.

9. It is proposed that the variety *N. frustulum* var. *minutula* be included under the species *N. frustulum* and that *N. frustulum* var. *perminuta* be retained as a variety.

10. Under the epithet *N. frustulum*, the following description would apply: valves mostly linear, occasionally somewhat linear-lanceolate, with sides varying from slightly concave to slightly convex; ends obtuse, attenuate-cuneate, sometimes slightly knob-like at the very end, but never capitate as such; length 10-ca. 50 μ , width 2.5-4 μ striae 22-ca. 24 in 10 μ , keel punctae 8-13 in 10 μ .

ACKNOWLEDGMENTS

The writer expresses sincere thanks to Dr. Ruth Patrick for aiding in the formulation of the study and for critical reading of the manuscript and to Miss Evelyn Wells for constructive editing comments. Thanks are also expressed to: Dr. M. H. Hohn, Mr. J. H. Wallace, Miss Marjorie E. Shipley, and Miss Marcia Levinsky who aided in various ways.

REFERENCES

1. ANDERSON, E. A., AND LESLIE HUBRICHT. The American sugar maples. I. Phylogenetic relationships, as deduced from a study of leaf variation. *Bot. Gaz.* 100(2): 312-323. 1938.
2. CLEVE, P. T., AND A. GRUNOW. Beiträge zur Kenntniss der arctischen Diatomeen. *K. Sv. Vet. Akad. Handl.*, Ser. 2, 17(2):1-121.7 pl. 1880.
3. DANSEREAU, PIERRE, AND ANDRÉ LAFOND. Introgression des caractères de *l'Acer saccharoprorum* K. Koch et de *l'Acer nigrum* Michx. *Contr. Inst. Bot. Univ. Montreal* 37:15-31. 1941.
4. GEITLER, L. Der Formwechsel der pennaten Diatomeen. *Arch. Protistenk.* 78(1):1-226. 1932.
5. HUSTEDT, F. Bacillariophyta (Diatomeae). Heft 10 in: *Die Süßwasser-Flora Mitteleuropas*, A. Pascher. Gustave Fischer, Verlag, Jena. 466 pp. 1930.
6. KÜTZING, F. T. Die kieselchaligen Bacillarien oder Diatomeen. Nordhausen. 152 pp. 30 pl. 1844.
7. PATRICK, RUTH. Sexual reproduction in diatoms. In: *Sex in micro-organisms*. Colonial Press Inc., Clinton, Mass., pp. 82-99. 1954.
8. VAN HEURCK, H. Synopsis des Diatomées de Belgique. *Atlas. J. Ducaju & Cie.*, Anvers. 132 pl. plus Suppl. 1880-1882.
9. WALLACE, JOHN H., AND RUTH PATRICK. A consideration of *Gomphonema parvulum* Kütz. *Butler Univ. Bot. Stud.* 9:227-234. 1950.
10. WIEDLING, STEN. Beiträge zur Kenntnis der vegetative Vermehrung der Diatomeen. *Bot. Not.* 3:322-354. 1948.

EXPRESSION OF THE GENE d_1 IN THE SCUTELLUM OF MAIZE

By JEANETTE S. PELTON

There have been many descriptions of the morphological expression of mutant genes in the mature plant body, but relatively little has been done on gene expression in early stages of ontogeny in higher plants. The fact that many genes have marked expression in older plants raises the question of the extent to which they are manifested at earlier stages of development. In the present study an embryonic structure of maize, the scutellum, is investigated for evidence of expression of a simple Mendelian recessive, dwarf-one (d_1). Four different inbreds were used because it was anticipated that quantitative expression of the gene would be modified by association with different genotypes. The scutellum was chosen as the specific subject of study since preliminary investigations indicated that scutellum shape varied from one inbred to another. It seemed possible, then, that a single gene difference might also show some expression in this organ.

Presence of the gene d_1 is clearly apparent at maturity; plants homozygous recessive for this gene are considerably lower in stature and have shorter and wider leaves than do their normal sibs (Abbe, L. 1936). The gene d_1 is located on the third chromosome and segregates in a three to one ratio (Emerson, Beadle, and Fraser 1935).

MATERIALS AND METHODS

Source of Materials:

The maize kernels used in this study were the product of a backcrossing program which has extended through a number of generations. The original material carrying the gene d_1 was backcrossed to four University of Minnesota Agriculture Experiment Station inbreds; A21, A25, A172, and A188. In summary, the breeding program that produced the segregating cultures is as follows:

1940	d_1d_1	♂	X	♀	Station Inbred	P_1
1941	D_1d_1	♂	X	♀	"	"
1942	D_1d_1	♂	X	♀	"	"

1944 $D_1d_1\delta$ X ♀ " " F_8 " " " " "
1945 $F_8\boxtimes$ (non-segregating progeny discarded) $F_8\boxtimes$
1948 $(F_8\boxtimes)\boxtimes$ (non-segregating progeny discarded) $F_8\boxtimes\boxtimes$

This program was essentially followed for all the inbred cultures, except that in A25 four generations of backcrossing rather than the usual three years preceded the two years of selfing.

Although normal sibs in the material segregating for d_1 differ slightly from the Station inbreds because of the introduction of the gene d_1 from a foreign background some three or four generations earlier, the Experiment Station's original designations will be used for the inbred cultures studied.

Characteristics of the Four Inbred Lines:

Field observations of the four Station inbreds for several generations have shown that the inbreds differ in certain seedling and mature plant characteristics. Major differences observed in characteristics of mature plants are height, leaf shape, and leaf color. A brief description of these differences is as follows: In height A25 is the tallest, A172 second tallest, A188 third, and A21 the shortest; leaf shape differs with A188 having the widest leaves, A21, A25, and A172 having narrow leaves, A172 being the narrowest; leaf color ranges from dark green in A188 to the lightest green of the group in A21. A25 differs from the other inbreds in having rather poor germination qualities as compared to the excellent germination qualities for the other three. Time of germination marks a definite distinction between the four inbreds; A21 germinates first, A172 second, A188 third, and A25 last. In addition to these differences the writer's measurements of the scutella from mature kernels show that the Station inbreds also differ in size and form of the scutellum in each line. The mathematical means for length, width, and depth of excised scutella are given in Table I.

Thus, mature plant characteristics as well as germination traits indicate genetic differences in the four Station inbreds. This genetic difference is also expressed in the scutellum with notable differences in form: A21 has the shortest scutellum, A188 the widest scutellum, and that of A172 has the greatest depth. Since such marked differences were correlated with major genetical differences, it seemed not unlikely that a single gene difference might also be expressed in the scutellum.

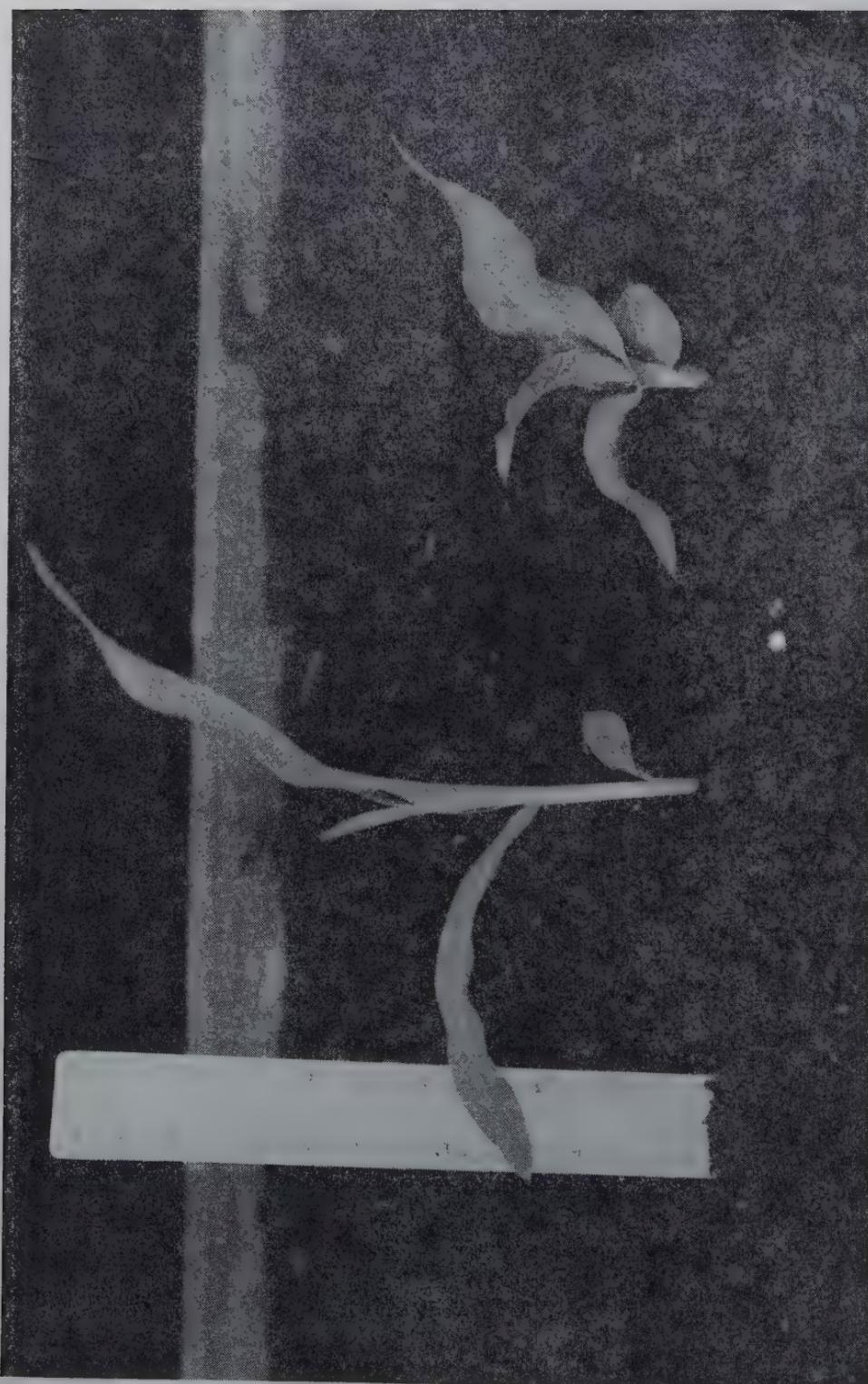


Fig. 1. Ten day old seedlings of a normal sib and the homozygous recessive dwarf-one of *Lathyrus sativus*. 1:1

Experimental Procedure:

Shelled kernels from a single ear of each of the four inbred segregating cultures were used and included about 200 to 250 kernels of each inbred culture. Throughout the experiments environmental conditions were kept as nearly uniform as possible. Simultaneous soaking of ten kernels of each inbred culture in distilled water was the first step of each experiment. Forty-eight hours later maximum length and width of scutellum and kernel were measured to 0.2 mm using 13.8X magnification. A critical feature in the experimental procedure was the determination of the genetical identity of each scutellum. This could be assured only by growing the plants until the characteristic difference in form of the seedling leaves permitted the identification of the homozygous recessives. Figure 1 illustrates this phenotypic difference in the ten day old seedlings. Therefore, each individual measured scutellum received a number which was given phenotypic identification at the seedling stage. Thirteen such experiments were completed between April 5, 1949 and June 5, 1949.

EXPERIMENTAL RESULTS

Average length of the scutellum in the dwarf embryos as compared with that of its normal sibs does not differ statistically in any of the four inbred cultures. Statistical treatment included calculation of mathematical mean, standard deviation, and the probability of significant differences between mathematical means. The latter calculation was made by using the following formula:

$$k = \frac{\bar{X}_1 - \bar{X}_2}{\sqrt{\frac{s_1^2}{N_1 - 1} + \frac{s_2^2}{N_2 - 1}}}$$

\bar{X}_1 and \bar{X}_2 refer to the means of the normal and dwarf measurements.

s_1^2 and s_2^2 refer to the square of the standard deviations of the two populations.

N_1 and N_2 refer to the numbers of individuals in the two populations.

k is the ratio between observed difference and its standard error and is used with a table of normal curve functions (Treloar 1939, pp. 240-243).

Only one case of a statistically significant difference in dwarf and normal means is found in scutellar width: That difference being the larger mathematical mean of the normal in the A21 culture, with a probability of 0.02%. These statistical results are summarized in Table II.

Analysis of length and width of the kernel dimensions using the same statistical treatment as in scutellar analysis did not produce any statistically significant differences between dwarf and normal mathematical means. Statistical results of kernel measurements are summarized in Table III.

DISCUSSION

Results of the present study indicate that although major genetical differences between inbred lines of maize may be reflected in scutellar size and form, similar differences were not correlated with d_1 in the homozygous recessive state. While the phenotype of this recessive gene is noticeably different from its normal sibs as early in development as the very young seedling, a corresponding expression in the scutellum is not found. Thus, the numerous genes that control size and shape of scutellum are found to differ in the Station inbreds, but an introduction of a single gene difference does not seem to alter any of these gene complexes at this early stage.

In view of this lack of expression of the gene d_1 in kernel as well as scutellar form, a consideration of the role of environmental influences seems in order. Among external factors that might alter kernel size and shape are: Nutrition, pressure of the surrounding kernels, and moisture and temperature during development of the kernels. An attempt was made to equalize such positional effects as pressure and distance from the vascular tissue supplying nutrients and water, and the resulting competition among the kernels, by using all the kernels from a single ear for each of the inbred lines. Moisture and temperature during development of the kernels are variables common to all four cultures because they were grown during the same season and in the same uniform field plots. Therefore, while external factors can be important in affecting kernel form, the in-

fluence of these factors would seem sufficiently uniform to the individuals in the experiment to rule out environmental conditions as a major factor in modifying genetic expression of a gene such as d_1 that so completely modifies many characteristics of maize.

Among the factors which might affect scutellar form the relationship between kernel form and scutellar dimensions should not be overlooked. A high correlation between scutellar and kernel dimensions might indicate that the caryopsis wall can have some influence on scutellar size. Scatter diagrams of kernel and scutellar length and width, however, indicate only weak correlations or none at all. Consequently, these data do not support the theory that surrounding tissues have some restricting action on embryo dimensions in this experiment.

The genetic composition of the scutellum in the material analyzed in the present study can be divided into three classes: The homozygous recessive, d_1d_1 , the homozygous dominant, D_1D_1 , and the heterozygous, D_1d_1 . This is in marked contrast to the genetic uniformity of the caryopsis wall which is consistently D_1d_1 . Interestingly enough, even though the seedlings which developed from the measured embryos could be classified either as phenotypically dwarf or normal, a corresponding phenotypic expression of d_1 in the scutellum is not found. Against three of the inbred backgrounds (A25, A188, and A172) the mathematical means of the scutella of the dwarf embryos did not differ statistically either in length or width. The only statistically significant difference is in the A21 strain in which the mathematical mean of the scutellum of the normal is larger in width than that of the dwarf. In this case the actual difference between dwarf and normal means is only 0.4 mm, which is a rather slight difference since measurements were made to only 0.2 mm. Thus, it would seem that the d_1 gene has little or no influence on the genes controlling embryonic size in either the dwarf or normal embryos. A possible explanation is that the threshold of action of d_1 may come after the completion of embryonic growth.

SUMMARY

The purpose of the investigation described above was to determine whether the gene d_1 is expressed in the mature embryo of maize. Four inbred lines, each segregating for the gene, were used

in the experiment. The method of study involved measurements of maximum length and maximum width of scutellum and kernel. Identification of the gene was possible through the use of a numbering system assuring the correct phenotype at the seedling stage. Statistical analysis of the data shows only one case of a statistically significant difference between normal and dwarf scutellar measurements and none in kernel measurements. Therefore, the present study indicates very little or no recognizable influence of the gene d_1 on those genes controlling scutellum and kernel growth in these early stages of ontogeny.

LITERATURE CITED

ABBE, L. B. The histological background for dwarfism in *Zea mays*. Proc. Amer. Phil. Soc. 76:743-747. 1936.

EMERSON, R. A., G. W. BEADLE, AND A. C. FRASER. A summary of linkage studies in maize. New York Agric. College (Cornell) Exper. Sta. Mem. 180:1-83. 1935.

TRELOAR, A. E. Elements of statistical reasoning. John Wiley and Sons. New York. 1939.

ACKNOWLEDGMENTS

Acknowledgments are gratefully extended to the following persons: Dr. E. C. Abbe for helpful advice throughout the study and in preparation of the manuscript, and for provision of the maize kernels used in this study; Dr. J. F. Pelton for valuable assistance throughout the study; Mr. D. Baer for statistical advice; Mr. J. M. Olmsted for testing the maize kernels used in this work for variability and segregation, and for descriptions of the mature plants of the Station inbreds; Dr. B. Phinney for description of the Station inbred mature plants; and to Dr. S. C. Reed for criticism of the thesis manuscript.

TABLE I

Mathematical means for measurement of 50 excised scutella of each Station inbred.

Station Inbred	Length	Width	Depth
A21	6.90mm	4.48mm	3.29mm
A25	7.81mm	4.22mm	3.05mm
A172	7.64mm	5.15mm	3.85mm
A188	7.82mm	5.54mm	2.86mm

TABLE II

Comparison of scutellar size between normal and dwarf individuals.

Inbred Culture	Pheno-type ¹	Number ²	Scutellar Length			Scutellar Width		
			Mean	Standard Deviation	Probab-ility ³	Mean	Standard Deviation	Probab-ility ³
A21	N	80	7.56	0.591	3.2%	5.93	0.616	0.02%
	D	24	7.75	0.280		5.47	0.500	
A25	N	94	7.24	0.761	81.8%	5.30	0.648	67.4 %
	D	32	7.20	0.670		5.25	0.538	
A172	N	83	7.06	0.761	58.9%	5.20	0.331	68.9 %
	D	39	7.12	0.447		5.16	0.565	
A188	N	72	8.31	0.501	2.5%	6.46	0.655	19.7 %
	D	33	8.59	0.616		6.30	0.538	

¹ N = Normal, D = Dwarf.² Total number of individuals included in study.³ Probability of the significant difference between means.

TABLE III

Comparison of kernel size between normal and dwarf individuals.

Inbred Culture	Pheno-type ¹	Number ²	Kernel Length			Kernel Width		
			Mean	Standard Deviation	Probab-ility ³	Mean	Standard Deviation	Probab-ility ³
A21	N	80	9.26	0.700	93.6%	7.01	0.538	39.0 %
	D	24	9.25	0.316		7.15	0.728	
A25	N	94	10.30	1.396	40.1%	7.53	1.126	42.4 %
	D	32	10.06	1.382		7.70	0.994	
A172	N	83	9.04	0.916	45.3%	8.48	0.883	2.2 %
	D	39	9.18	0.979		8.81	0.655	
A188	N	72	10.22	0.761	32.7%	9.33	0.932	77.2 %
	D	33	10.38	0.774		9.38	0.728	

¹ N = Normal, D = Dwarf.² Total number of individuals included in study.³ Probability of the significant difference between means.

POST-ALGONQUIN AND POST-NIPISSING FOREST HISTORY OF ISLE ROYALE, MICHIGAN*

By J. E. POTZGER

Isle Royale, the largest island in our Great Lakes, is located in the northwestern part of Lake Superior, 50 miles nw. of the Keweenaw Peninsula, 20 miles se. of the Canadian mainland, and 19 miles east of Grand Portage, Minnesota. Maximum elevation is 1300 feet, but most of the higher central ridge does not exceed 1,000 feet. Present altitude of Lake Superior is 602 feet.

The island is a national park, to be kept as a wilderness area without roads. But here as well as in the vast untouched forest regions of Quebec, lightning-ignited fires have destroyed much virgin timber and have reduced succession to initial primary status on bare rock surfaces. The writer could not escape the impression that most of the island has been burned over in the not too distant past. Deep fjord-like harbors and coves as well as numerous barrier chains of islands constitute striking peripheral features.

Isle Royale presents a rugged, much deformed and uptilted rock formation with the scars of glaciation still plainly visible. Soil constitutes an extremely thin veneer on pre-Cambrian rocks. Nowhere has the writer seen more windfall damage to forests. For the palynologist Isle Royale is of interest because during Mankato time Algonquin and Nipissing high water stages of Lake Superior submerged much of the Keweenaw Peninsula and most or all of Isle Royale. Thus the forest history recorded in peat of bogs on the island could not record all of post-Mankato time, but surely all of post-Algonquin and post-Nipissing times. It was therefore assumed that the earliest forest history recorded in the bogs on the mainland, which was above the altitude of submergence should be wanting on Isle Royale. Also, if process of emergence was slow, one might find variation in forest succession in bogs of higher and lower elevations.

* This is publication 278 from the Botanical Laboratory of Butler University.

During the summer of 1948 nine bogs were bored, two of these were at or below the present lake level (Raspberry Island bog and Senter Point bog). The others ranged from 625 to 900 feet in elevation. All bogs except the Raspberry Island kettle had very shallow peat deposits.

DESCRIPTION OF BOGS

SISKIWIT MINE BOG: located at T 64 N., R 37 W., Sec. 20 (se. corner), borders on the Siskiwit Copper Mine. *Picea mariana* and *Thuja* were on the bog mat. *Acer saccharum*, *Betula lenta*, *A. rubrum* and *A. spicatum* were present on surrounding uplands.

ANGLEWORM LAKE BOG: T 66 N., R 34 W., Sec. 22, represented the valley-type bog. It was near Angleworm Lake along the Ojibway trail. The mat has a dense cover of *Picea mariana* (Black spruce).

FORBES LAKE BOG: T 66 N., R 34 W., Sec. 27 (nw. corner). It is a small circular bog with open Sphagnum mat. Black spruce is invading and Chamaedaphne forms a dense shrub cover.

MOOSE LAKE BOG: T 66 N., R 34 W., Sec. 6 (sw. corner), is one depression in a series of boggy places between rocky uplands. It has a sparse tree cover (black spruce, arbor vitae) with intermittent open areas covered with Sphagnum. It is located nw. of Rock Harbor lodge, in the first valley beyond Tobin's Bay.

TOBIN'S HARBOR BOG: T 67 N., R 33 W., Sec. 34. It is a valley-type bog one mile north-east of Rock Harbor lodge. A rocky ridge separates it from Tobin's Bay. *Picea mariana* has a dense stand on the mat while the upland forest consists chiefly of *Betula papyrifera* and *Picea glauca*.

HOUGHTON POINT BOG: T 63 N., R 37 W., Sec. 3, is a small oblong bowl covered with dense stand of black spruce and paper birch.

ROCK HARBOR BOG: This is an oblong depression separated from the lake by a 50-foot wide rock wall. Black spruce and arbor vitae control the forest cover.

SENTER POINT BOG: T 64 N., R 37 W., Sec. 33 (ne. corner), apparently originated as a beach pool. At present it is separated from the lake by 100 feet or more of a sandy gravel bar. The center is a sedge meadow and Sphagnum. The surrounding forest is primarily *Picea mariana*.

RASPBERRY ISLAND BOG: The island is about one mile south east of Rock Harbor lodge. The bog has a fine Sphagnum mat with scattered Chamaedaphne and Ledum shrub layer. The bordering forest consists chiefly of spruce, fir and paper birch.

METHODS

The Hiller-type borer was used in the field sampling. Boring was continued in every bog until compacted sand or rock stopped the operation. Peat samples were placed into carefully marked vials and stoppered securely. In the laboratory the Geisler (6) alcohol method was used to separate the peat. Counts of 200 tree pollens were made at most foot-levels. Pollens of herbaceous plants and spores of Pteridophytes were counted but have not been included in the graphs.

RESULTS

Figures 1 and 2 present the forest history in a summary manner. According to Leverett and Taylor (8) and Flint (4) Isle Royale was submerged entirely by Algonquin high water stage, and in part during Nipissing times. This made the conclusion obvious that early forest history of the region as a whole could not be represented in its entirety in the profiles of bogs from the island. This is clearly shown by the lowest levels of the bogs (Figs. 1, 2) when comparison is made with bogs from nearby Minnesota (10) and Michigan (11). Either the transition pine-spruce or the pine periods were in control at the time sedimentation began in the Isle Royale bogs. All profiles ended in a spruce-pine-birch forest association. Raspberry Island and Senter Point (Fig. 2, bogs 8, 9) bogs originated at a time when lake level was not higher than at present and so should show only the most recent history. In a general way the profiles present three types of forest history (Figs. 1, 2) all culminating in similar forest association. Bogs at 700 to 900 foot elevation (Fig. 1, bogs 1, 2, 3) record the close of the initial spruce-fir period (this association is characteristic for the region), they also indicate the bimodal pattern of spruce-fir which characterizes the profiles from the mainland. Bogs at 625-650 foot elevation (Fig. 2, bogs 3-7) indicate spruce-fir rising from a decided low to a prominent peak at the close, a pattern appearing in bogs at 700 to 900 foot elevation in the upper half of their profiles. The bogs at 600 foot elevation (Fig. 2, bogs 8, 9) show a rather uniform abundance of spruce in the

whole profile, thus recording only the more recent history of spruce and fir.

In bogs at highest elevation *Tsuga* is present chiefly in the upper third of the profiles; it spreads its representation to 3/4 of the profiles of bogs at 625-650 foot elevation, and is present in the whole profile in bogs at present lake level. *Abies* (fir), in greater abundance, shows the same distributional pattern. Fir indicates greater importance in the forest history of the island than on the mainland of Minnesota (9). The best expressed xerothermic period is no doubt represented by the pine climax and the low oak peak near the close of the pine period. While low percentages of hemlock may indicate long distance transfer from the mainland, the higher percentages no doubt indicate former presence of *Tsuga* on the island. Both hemlock and birch have their highest representation at the close of the pine period.

A summary of cardinal points of the various bogs is here given for ready reference:

Bogs	Elevation Ft.	Depth of Peat	Initial Forest
Siskiwit Mine bog	900	4 feet, 11 in.	pine-spruce
Angleworm Lake	800-850	7 feet, 2 in.	pine (spruce)
Forbes Lake	700-750	5 feet	pine
Moose Lake	650	4 feet, 6 in.	pine
Tobin's Harbor	650	6 feet	pine
Houghton Point	625	5 feet, 6 in.	pine-spruce-birch
Rock Harbor	625	7 feet, 3 in.	pine
Senter Point	600	4 feet, 6 in.	pine-spruce-fir-birch
Raspberry Island	600	13 feet, 11 in.	pine-spruce-birch

Note: Elevations according to U. S. Lake Survey Chart 981 (14).

DISCUSSION

Isle Royale has a fascination for geologists as well as for biologists. Copper mining was in operation as early as 1844, and the University of Michigan sent an expedition to the island in 1908 (Adams (1) pp. 1-53) to study the biota found on the island. Isle Royale is separated from the mainland at least 20 miles at the nearest point, and this must no doubt present migration problems for both plants and animals. The classical survey of the forests by Cooper (3) in 1913 brought the forest ecology of Isle Royale to the attention of the world. One is somewhat surprised that migration diffi-

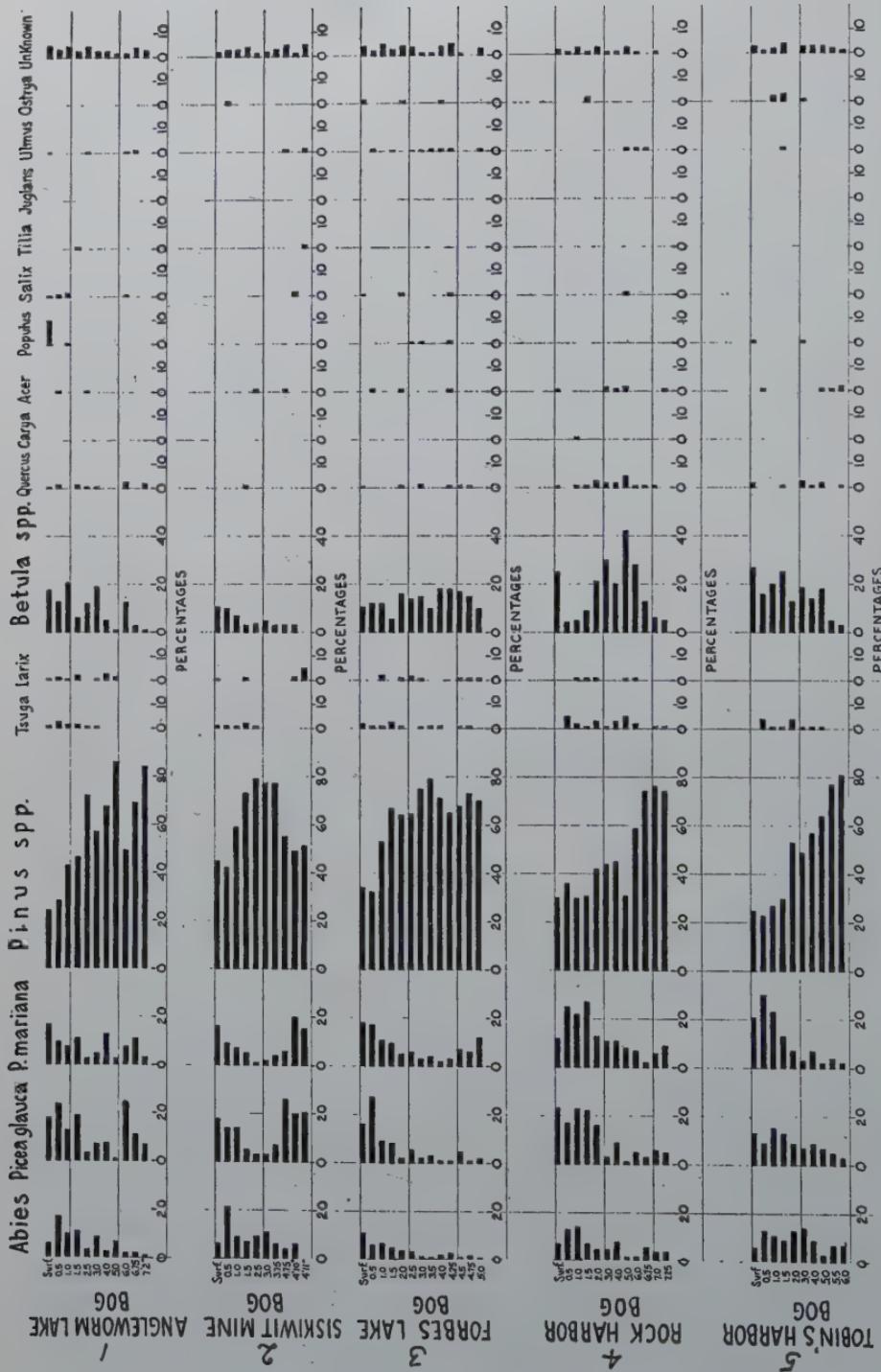


Fig. 1. Profiles from bogs 1, 2, 3, 4, 5.

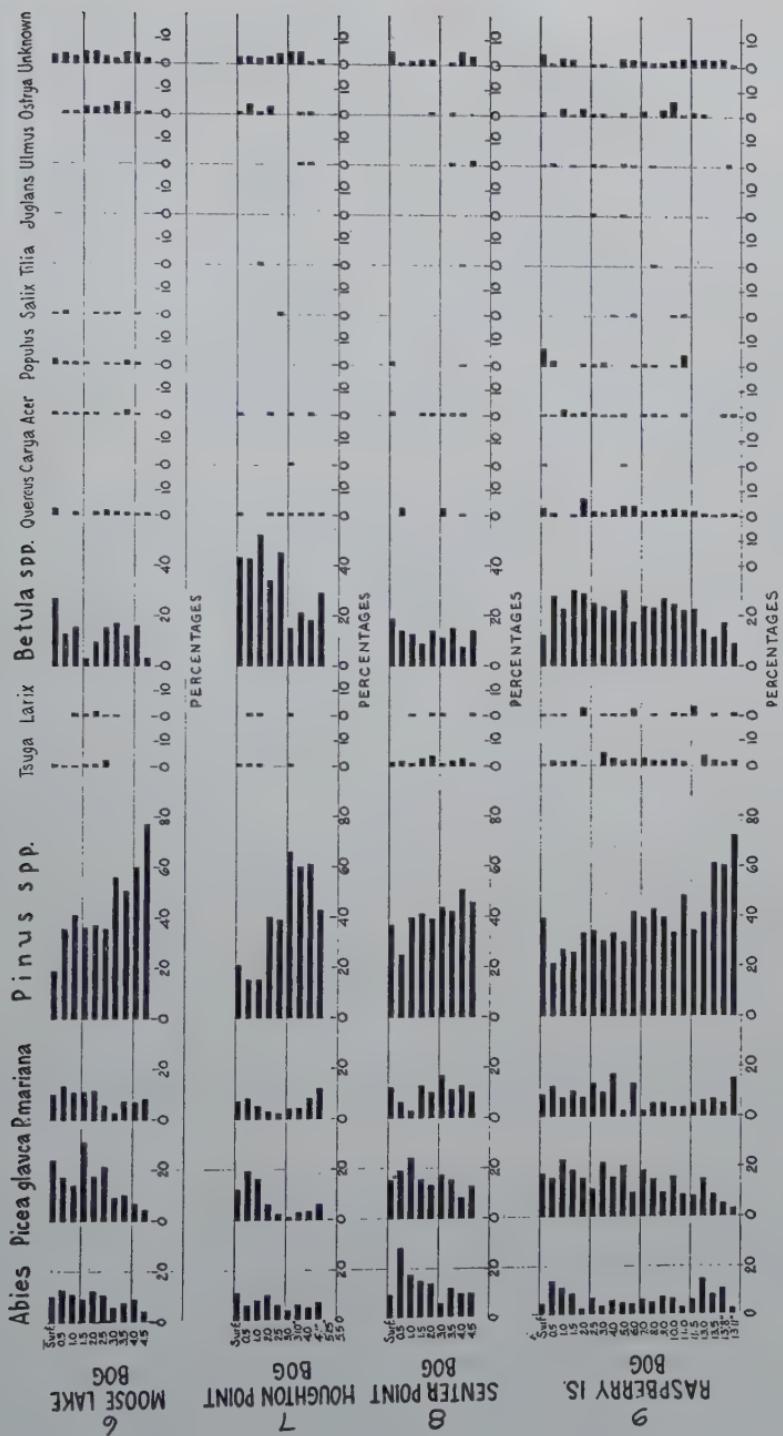


Fig. 2. Profiles from bogs 6, 7, 8, 9.

culties permitted so many plant species to become established on this rocky outpost. Brown (2) lists a total of 671 species of ferns and flowering plants. Of these 26 are trees (8 evergreens) and 87 are shrubs. Cooper (3) lists the island as the northernmost station for sugar maple (*Acer saccharum*) for that part of North America. While sugar maple reaches a higher latitude in the Saguenay valley of Quebec, it still remains a critical location for certain broadleaved genera. The same author considers *Abies*, *Picea glauca* and *Betula papyrifera* as climax forest association. The pollen profiles support such conclusions, for it is very evident that even though pine has still a significant representation its climatic climax has been replaced by spruce-fir climax.

For the present study the most important item for consideration was that on Isle Royale the palynologist had an opportunity to fit post-Algonquin and post-Nipissing time into the forest history of nearby mainland locations which were above the high water stages of Lake Superior. According to Leverett (7) and Leverett and Taylor (8) Algonquin water covered the island completely and Nipissing submergence reached 656 foot elevations. From the pollen profiles we know that earliest post-Algonquin forest history began at the close of the spruce-fir period and at the beginning of the pine climax, which in this location no doubt also represents the major xerothermic period. One is also justified to correlate the pine climax on the island with that on the mainland as reported by Potzger (10) for the Quetico-Superior forest region. A carbon-dating by Libby (9) for the Johnson Camp bog in Minnesota placed the pine period initiation at 7128 (plus or minus 300 years). Since the Quetico-Superior forest lies in the same latitude as nearby Isle Royale, we should be justified to assume the same age for the pine period on Isle Royale.

In the bogs from the post-Nipissing time (Bogs 4, 5, 6, 7) one should expect decline of spruce and fir because the continued wasting of the ice northward must be an indicator of warming climate (major xerothermic period). It is, of course, interesting that waning climax of pine and gradual increase of spruce and fir also marks the close of Nipissing times (Fig. 2, bogs 8, 9), so that in the Lake Superior region Nipissing time is represented by the maximum pine peak, including at least a portion of its rise and decline. Since the general

pattern of forest history on higher elevations of Isle Royale (Fig. 1, bogs 1, 2) is so similar to that of southern Quebec, as shown by Potzger (12) and Potzger and Courtemanche (13), one is inclined to assume that forests of both regions began during early post-Algonquin time, and both locations experienced the pine maximum up to the period of obvious decline during Nipissing times. Potzger (12) came to this conclusion while analyzing the geological happenings in the St. Lawrence valley. To all appearances, lower Quebec could not have been invaded by forests until close of Algonquin IV, and the beginning of the xerothermic period. While in all profiles from Isle Royale spruce and fir did not decline to such low representation in mid-profile as in Quebec, bogs above 700 foot elevation show the same bi-modal tendencies for spruce as the Quebec bogs, and those of the Quetico-Superior area. Rise of spruce and fir in upper third of profiles indicates a cooling climate during more recent times. The study by Potzger (10) in Minnesota, Ontario, and in Gogebic county, Michigan (11) plainly show the early prominent spruce-fir dominance following Mankato retreat. Preliminary examination of peat from the lowest levels of bogs on the Keweenaw Peninsula, Michigan by the writer indicates more truncation of forest record there than on Isle Royale (700 to 900 foot elevation) because hemlock (*Tsuga*) plays a prominent role already in lowest levels. These bogs began during early post-Nipissing times. According to Leverett and Taylor (8) Nipissing waters covered the Keweenaw peninsula up to 600 foot elevation.

SUMMARY

1. The study presents nine pollen profiles from bogs on Isle Royale, Michigan, ranging in elevation from Lake Superior (602 feet) up to 900 feet.
2. It is assumed that because of complete submergence of Isle Royale during Algonquin times, and up to 656 foot elevation during Nipissing times these bogs record the forest history of post-Algonquin as well as of post-Nipissing times.
3. Three distinct patterns of forest, determined by elevation of bogs, are interpreted as marking post-Algonquin, post-Nipissing and the stability of the present lake level.

4. Algonquin IV apparently closed when pine replaced spruce-fir, as shown by comparison with early forest history of the bogs from the Quetico-Superior forest region and with those from Gogebic County, Michigan.

5. Nipissing time is represented by the rise, dominance and beginning of decline of pine.

6. Climate cooled during the time that the upper fourth of the sediments in the bogs accumulated. This is indicated by marked rise in spruce and fir.

7. While oak never was very abundant on Isle Royale, decline occurred during deposition of the upper levels marked by cooling climate.

8. All bogs record essentially the same forest composition in the upper foot-levels, indicating that differences in altitude on the island are not significant control factors in forest composition during the recent past. Upper levels indicate a forest similar to that found on the island today.

ACKNOWLEDGMENTS

Sincere thanks is expressed to the American Philosophical Society for grant 1062 (1948) to cover expenses for an assistant in the field work. Grateful recognition is aslo made of the following aid: Information on Isle Royale by Dr. C. C. Adams; arrangements for transportation on the Tonawanda to Siskiwit Bay by Mr. Charles E. Shevlin, superintendent of the park; information and maps provided by Mr. Charles Humberger; efficient help in the field work and use of his outboard motor provided by my assistant, Mr. Walter Lauterbach, Central High School, South Bend, Indiana. Thanks is expressed to Mr. Edward A. Rumely of New York for stimulating interest in the work and for gift of launch service to distant locations on the island, and to my wife for preparation of graphs for figures 1 and 2.

LITERATURE CITED

1. ADAMS, C. C. Isle Royale as a biotic environment. Rept. Univ. Mich. Museum State Biol. Surv., as a part of Rept. Geol. Surv. 1908.
2. BROWN, CLAIR A. Ferns and flowering plants of Isle Royale, Michigan. U. S. Dept. Interior. Emergency Conservation, Field Surv. Univ. Michigan Herbarium. 1933.

3. COOPER, W. S. The climax forest of Isle Royale, Lake Superior, and its development. *Bot. Gaz.* 55:1-44, 115-140, 189-235. 1913.
4. FLINT, RICHARD FOSTER. *Glacial Geology and the Pleistocene Epoch.* John Wiley and Sons, N. Y. 1945.
5. FLINT, RICHARD FOSTER ET AL. *Glacial map of North Am.* Geological Society of Am. New York. 1945.
6. GEISLER, FLORENCE. A new method for separating fossil pollen from peat. *Butler Univ. Bot. Stud.* 3:141-146. 1935.
7. LEVERETT, FRANK. Moraines and shore lines of the Lake Superior region. *U. S. Geol. Surv., Professional paper* 154 (pp. 1-72). 1929.
8. LEVERETT, FRANK AND F. B. TAYLOR. The Pleistocene of Indiana and Michigan, and the history of the Great Lakes. *U. S. Geol. Surv., Monograph* 53. 1915.
9. LIBBY, WILLARD F. Radiocarbon dating. *Univ. Chicago press* (p. 87). 1952.
10. POTZGER, J. E. History of the forests in the Quetico-Superior country from fossil pollen studies. *Jour. Forestry* 51:560-565. 1953.
11. ———. Pollen spectra from four bogs on the Gillen Nature Reserve along the Michigan-Wisconsin state line. *Am. Midland Nat.* 28:501-511. 1942.
12. ———. Nineteen bogs from southern Quebec. *Can. Jour. Botany* 31:383-401. 1953.
13. ——— AND ALBERT COURTEMANCHE. Bog and lake studies on the Laurentian Shield in Mont Tremblant Park, Quebec. *Can. Jour. Botany* 32:549-560. 1954.
14. U. S. Lake Survey. Isle Royale, Michigan. *Lake Superior Chart* 981. 1948.
15. U. S. Dept. Conservation. Geological Survey Div., Isle Royale Base Map 3460. 1935.

BUTLER UNIVERSITY BOTANICAL STUDIES

Edited by

J. E. POTZGER

VOLUME XI

1953-1954

PUBLISHED AND FOR SALE BY THE
DEPARTMENT OF BOTANY
BUTLER UNIVERSITY
INDIANAPOLIS 7, INDIANA
U. S. A.

W. J. Haw.